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THE UNIVERSITY OF ALBERTA

LIMIT CYCLES IN GAUSE-TYPE PREDATOR-PREY SYSTEMS

by

© Yang Kuang

A THESIS SUBMITTED TO

THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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FOR THE DEGREE OF

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Limit Cycles in Gause-Type Predator-Prey Systems submitted by Yang Kuang in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

H. I. Freedman

Supervisor

Date June 17/88

To Geoffrey J. Butler

ABSTRACT

Since the paper of May (1972) and Albrecht, Gatzke and Wax (1973) have appeared, one of the open problems in mathematical modeling of ecological systems has been the question of how to determine conditions which guarantee uniqueness of limit cycles in predator-prey models. Questions related to nonuniquness, period and location of limit cycles of predator-prey systems are also of much interest.

The first part of the thesis deals with the question of uniqueness of limit cycles in predator-prey systems of Guase type. By utilizing several transformations, these systems are reduced to a generalized Liénard system as discussed by Cherkas and Zhilevich, and Zhang. As a consequence, criteria for the uniqueness of limit cycles are derived, which include results of Cheng and is related to results of Liou and Cheng. Several examples are given to illustrate our results.

The central question in the second part of the thesis is the nonuniqueness of limit cycles of Guase-type predator-prey systems. By comparing with the Lotka-Volterra system, we obtain a theorem concerning the nonuniqueness of limit cycles of a Gause-type predator-prey system. The method we develop in this part can be generalized. Moreover, we disprove a conjecture posed by H.I. Freedman by constructing an example of a system with a strictly concave down prey isocline which has at least three limit cycles.

In the last part of the thesis, an attempt is made to estimate the location and period of the limit cycles of Gause-type predator-prey systems in the case

when there is a unique unstable positive equilibrium. An annular region which contains all the limit cycles is determined, and an upper bound for the period of the limit cycles is given. Both the annular region and the upper bound of the period are explicitly computable.

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CHAPTER I

INTRODUCTION

Models of Gause-type predator-prey systems were introduced by Gause (1934) and Gause, Smaragdova and Witt (1936) to help analyze paramecium-didinium interactions. Since then, various forms of these models (both continuous and discrete) have been utilized by many experimental and field biologists in studying predator-prey interactions. Some examples are those utilized by Armstrong (1976, 1979), Hassell (1978), Hassell and May (1973), and Rosenzweig (1969, 1971, 1973). Meanwhile, there have been many mathematicians attracted to the mathematical analysis of these models (see the references contained in Freedman (1980)). However, most of the previous work done were about the existence and local stability of equilibria or limit cycles. Results on the global analysis of these systems are very few, especially in the case when these systems possess at least one limit cycle. Questions concerning the uniqueness and nonuniqueness, location and period of limit cycles in Gause-type predator-prey systems are rarely considered.

Although the local stability analysis is essential in order to understand the corresponding models, it is not enough. A good understanding of a system largely depends on the availability of the detailed global analysis of the qualitative nature of the corresponding mathematical model. It is the purpose of this thesis to carry out such a systematic global analysis for the Gause-type predator-prey systems. Our emphasis is on the theory of limit cycles of these systems.

The system to be considered in this thesis is described by a system of plane autonomous ordinary differential equations. Although it is not of the most general Kolmogorov-type or one which involves time delays or diffusion, this system certainly includes many models utilized by experimental and fields biologists. For examples, see the papers perviously mentioned.

It is well known that Hilbert's sixteenth problem concerning the maximum number of limit cycles for the equation

$$\frac{dy}{dx} = \frac{Q_n(x,y)}{P_n(x,y)}$$

(where P_n and Q_n are polynomials of real variables x, y with real coefficients) is one of the hardest mathematical problems of this century. So far, very little progress has been achieved in solving this question. From this fact one may ascertain that any meaningful and systematic limit cycles analysis of Gause-type predator-prey system could be very difficult.

This thesis is organized as follows. In Chapter II, we first present a detailed description of our model, both biologically and mathematically. Then we carry out the local stability analysis of the system, namely the existence and stability of equilibria, which can be viewed as the first step towards the understanding of our system. In section 2.4, we introduce the well known Rosenzweig and MacArthur's criterion for determining stability of the interior equilibrium of a Gause-type predator-prey system. This criterion will be utilized frequently in our thesis. Section 2.5 contains a detailed phase plane analysis and results about the positive invariance and dissipativity of the system. In section 2.6, we have listed several

global stability results without any rigorous proofs. Although most of these global stability results are new in form, they can be derived without much change from the proofs of their corresponding counterparts in slightly different systems. In the last section, we have collected some general results on the theory of limit cycles in plane autonomous systems which are very helpful for the purpose of understanding our system in its various aspects. Again, several of these results are the author's own.

In Chapter III, we deal with the question of uniqueness of limit cycles in Gause-type predator-prey systems. By utilizing several transformations, these sytems are reduced to a generalized Lienard system as discussed by Cherkas and Zhilevich (1970), and Zhang (1986). As a consequence, criteria for the uniqueness of limit cycles are derived, which include results of Cheng (1981) and is very much related to results of Liou and Cheng (1987). Several examples are given to illustrate our results.

The central question of Chapter IV is the nonuniqueness of limit cycles in Gause-type predator-prey systems. By comparing with the Lotka-Volterra system, we obtain a general theorem concerning the nonuniqueness of limit cycles in Gause-type predator-prey system. Moreover, we disprove a conjecture posed by H.I. Freedman by constructing an example of a system with a strictly concave down prey isocline which has at least three limit cycles.

In Chapter V, an attempt is made to estimate the location and period of the limit cycles of Gause-type predator-prey systems in the case when there

is a unique unstable positive equilibrium. An annular region which contains all the limit cycles is determined, and an upper bound for the period of the limit cycles is given. Both the annular region and the upper bound of the period are explicitly computable.

The final chapter contains the concluding discussion and remarks. Three conjectures are posed.

To assist the reader to gain a better understanding of the material discussed in this thesis, we have included various related results in analysis and differential equations in the appendix. A comprehensive list of refrences is also included.

In this thesis, we have adopted the following notations:

R denotes the set of real numbers.

$R^n = \{(x_1, x_2, ..., x_n);\ x_i \in R\,,\ i = 1, ..., n\}$.

The first orthant is denoted by

$R^n_+ = \{(x_1, x_2, ..., x_n) \in R^n,\ x_i \geq 0,\ i = 1, ..., n\}$.

The positive cone is the interior of the first orthant.

$B \setminus A = \{x \in B \setminus x \notin A\}$.

Any other notation is either standard in mathematics or is defined explicitly when it first appears in the thesis.

CHAPTER II

PRELIMINARIES

2.1 Introduction

In order to understand limit cycles in predator-prey systems, it is necessary to undertake a detailed analysis of the dynamics of the model in various ways.

We begin the analysis in the next section by first establishing the model, including both mathematical and biological explanations. Although the class of predator-prey models considered in this thesis is not the most general Kolmogorov type, and it does not contain many other features that are sometimes required (eg. periodic coefficients, time delays, diffusion terms, etc), it certainly includes many models utilized by experimental and field biologists in studying predator-prey interactions. Models of the type studied here were introduced (Gause 1934, Gause, Smaragalova and Witt 1936) to help analyze paramecium-didinum interactions. Since then, various forms of these models (both continuous and discrete) have been utilized by Armstrong (1976, 1979), Hassell (1978), Hassell and May (1973), Rosenzweig (1969,1973), etc. in various studies of predator-prey systems.

In section 2.3, we discuss the existence and stability of equilibria, in a manner similar to the methods in Freedman (1980, Ch. 4). The graphical method of Rosenzweig and MacArthur is described in detail. In section 2.5, we prove the positive invariance and the dissipativeness of our Gause-type predator-prey system, and carry out a complete phase plane analysis for the first quadrant.

Section 2.6 deals with a series of global stability results for the unique positive equilibrium of the Gause-type predator-prey system. Most of these results have counterparts which have appeared in the literature for more restrictive models. However, Theorems 2.8 and 2.9 are new. Although no detailed proofs are given, the interested reader should be able to verify the proofs from the relevant references.

The final section of this chapter constains a brief introduction of the general theory of limit cycles in plane autonomous systems. Most of the material here comes from the recent book "Theory of Limit Cycles" (Ye et al, 1986). However, Theorems 2.11 and 2.13 are new.

For the remainder of this thesis, we adopt the following derivative notation, namely that "$\cdot$" $= d/dt$, whereas "$'$" stands for derivative with respect to the argument (e.g. $f'(z) = df(z)/dz$).

2.2 The model

In Gause (1934) and Gause et al (1936) the following model was considered as a model of predator-prey interactions

$$\begin{aligned} \dot{x} &= \alpha x - yp(x), \quad x(0) = x_0 \geq 0 \\ \dot{y} &= y(-\gamma + cp(x)), \quad y(0) = y_0 \geq 0 \end{aligned} \tag{2.1}$$

where α, γ, c are positive constants. In Freedman (1980, Ch. 4), a more general form of (2.1) as an intermediate model of predator-prey interactions was analyzed in some detail. This model takes the form

$$\begin{aligned} \dot{x} &= xg(x) - yp(x), \quad x(0) = x_0 \geq 0 \\ \dot{y} &= y(-\gamma + q(x)), \quad y(0) = y_0 \geq 0 \end{aligned} \tag{2.2}$$

In the present thesis, we consider a further generalized model than that given by (2.1), the so called Gause-type predator-prey model. It has the following form:

$$\begin{aligned} \dot{x} &= xg(x) - \xi(y)p(x), \quad x(0) = x_0 \geq 0 \\ \dot{y} &= \eta(y)(-\gamma + q(x)), \quad y(0) = y_0 \geq 0 \end{aligned} \tag{2.3}$$

We think of $x(t), y(t)$ as representing the prey and predator populations, respectively, at given time $t \geq 0$. Here $g(x)$ is the specific growth rate of the prey in the absence of any predators and $p(x)$ is the predator response function for the predator with respect to that particular prey. γ is the death rate of the predator in the absence of its food.

Throughout this thesis, we assume $g(x), \xi(y), p(x), \eta(y), q(x)$ are continuously differentiable, so that existence, uniqueness and continuability for all positive t is satisfied for initial value problems.

The assumptions on $g(x)$ are

(H1): $g(0) > 0$; there exists $K > 0$, such that $g(K) = 0$, and $g(x) > 0$ on $0 \leq x < K$, $g(x) < 0$ on $x > K$. Moreover, we assume $g'(K) < 0$. K is called the carrying capacity of the environment.

These assumptions are, of course biologically realistic and mathematically general.

For $p(x)$, we assume

(H2): $p(0) = 0$, $p'(x) > 0$, for $x \geq 0$.

Similar assumptions are made with respect to $q(x)$, $\xi(y)$ and $\eta(y)$.

(H3): $q(0) = 0$, $q'(x) > 0$, for $x \geq 0$.

(H4): $\xi(0) = 0$, $\xi'(y) > 0$, for $y \geq 0$.

(H5): $\eta(0) = 0$, $\eta'(y) > 0$, for $y \geq 0$.

The first equation of (2.3) states that the prey growth is enhanced by its own presence in a manner analogous to single-species growth and is diminished by an amount proportional to the number $\xi(y)$ multiplied by the predator response function $p(x)$.

In Gause's model (2.1), $q(x) = cp(x)$. It will be helpful to think of $q(x)$ in this manner.

The second equation of system (2.3) describes the growth of the predator population. In the absence of prey, the predator population declines. The growth is enhanced by the presence of prey by an amount proportional to the number of prey. In some sense, $q(x)$ may be interpreted as the proportion of prey eaten which becomes converted into predator. This proportionality may vary with prey density. If not, then indeed $q(x) = cp(x)$.

Note that in the special case that $\xi(y) = \eta(y) = y$, (2.3) reduces to (2.2). We remark that a new feature of such predator-prey models is incorporated by allowing $g'(0) > 0$. This represents a prey population which can exhibit an accelerated population specific growth rate for intermediate values of population

as a strategy to avoid extinction. Moreover, (2.3) also allows for the possibility of mutual interference among predators.

Some of the specific forms of $g(x)$ and $p(x)$ frequently used are:

$$g(x): \quad r(1-\frac{x}{K}); \quad \frac{r(K-x)}{K+\epsilon x}; \quad r[1-(\frac{x}{K})^c], \quad 1>c>0,$$

$$p(x): \quad \frac{mx^n}{a+x^n}, \quad n \geq 1; \quad mx^c, 1 \geq c > 0; \quad m(1-e^{-cx}), \quad m>0, \quad c>0.$$

while $\xi(y), \eta(y)$ frequently takes one of the form αy or αy^m, $0 < m < 1$.

2.3 Existence and stability of equilibria

Assuming (H1) to (H5), we see that (2.3) always has at least two equilibria, namely $E_1(0,0)$ and $E_2(K,0)$.

The equilibrium of greatest interest would be an equilibrium interior to the first quadrant of the $x-y$ plane, so we try to find conditions for such an equilibrium to exist. We denote this equilibrium by $E^*(x^*, y^*)$, where $x^* > 0$, $y^* > 0$.

We denote $q_\infty = \overline{\lim}_{x\to\infty} q(x)$. Then $0 < q_\infty \leq \infty$. Now note that x^* and y^* satisfy

$$\begin{aligned} x^* g(x^*) - \xi(y^*)p(x^*) &= 0 \\ \eta(y^*)(-\gamma + q(x^*)) &= 0 \end{aligned} \tag{2.4}$$

Therefore we require $-\gamma + q(x^*) = 0$. Since $q'(x) > 0$, when $x > 0$, it must occur that

$$-\gamma + q_\infty > -\gamma + q(x^*) = 0$$

i.e.

$$q_\infty > \gamma \tag{2.5}$$

Biologically, this is necessary for the persistence of the ecosystem, for if $q_\infty \leq \gamma$, then $-\gamma + q(x) < 0$, for all $x > 0$, and $\dot{y} < 0$. Hence $y(t)$ is a decreasing function and therefore there exists $y_0 \geq 0$, $y_0 \geq \lim_{t\to\infty} y(t)$ and $\overline{\lim}_{t\to\infty} \dot{y}(t) = 0$. However, if $y_0 > 0$, then $\lim_{t\to\infty} \dot{y}(t) < \eta(y_0)(-\gamma + q(K+1)) < 0$, since eventually $x(t)$ will be in the interval $(0, K]$, and $q'(x) > 0$, if $x > 0$. Hence $y_0 = 0$. This implies that the predator species goes extinct.

By assuming (2.5), we see that there is a unique $x^* > 0$, such that

$$q(x^*) = \gamma . \tag{2.6}$$

However, as we stated above,

$$\overline{\lim}_{t\to\infty} x(t) \leq K \tag{2.7}$$

Hence, we require $x^* \leq K$.

By solving y^* in terms of x^* in the first equation of (2.4), we obtain

$$y^* = \xi^{-1}\left(\frac{x^* g(x^*)}{p(x^*)}\right) \text{ provided } \lim_{y\to\infty} \xi(y) > \frac{x^* g(x^*)}{p(x^*)} .$$

Since we require $y^* > 0$, it follows that $g(x^*) > 0$ which requires $x^* < K$.

Biologically, if $x^* \geq K$, then the predators again go extinct. For even in the absence of predators the prey population is bounded above by K or decreases to K if initially greater than K. With predators present, the population will be brought below K and stay below. It is easy to see that if $q(K) - \gamma < 0$, then

$\lim_{t\to\infty} y(t) = 0$, in which case $\lim_{t\to\infty} x(t) = K$, i.e. solutions initiating in the interior of the positive cone will approach $(K,0)$ asymptotically. Therefore, from now on, we assume:

(H6) there exists x^*, $0 < x^* < K$ such that $q(x^*) = \gamma$,

(H7) $\lim_{y\to\infty} \xi(y) > x^* g(x^*)/p(x^*)$.

To analyze the stability of the equilibria $E_1(0,0)$, $E_2(K,0)$, $E^*(x^*,y^*)$, we need to compute the variational matrix (Jacobian) of (2.3). This take the form

$$M(x,y) = \begin{bmatrix} xg'(x) + g(x) - \xi(y)p'(x) & -\xi'(y)p(x) \\ \eta(y)q'(x) & \eta'(y)(-\gamma + q(x)) \end{bmatrix} \tag{2.8}$$

For $E_1(0,0)$, $M(x,y)$ reduces to

$$M(0,0) = \begin{bmatrix} g(0) & 0 \\ 0 & -\gamma\eta'(0) \end{bmatrix} \tag{2.9}$$

whose eigenvalues are $g(0)$ and $-\gamma\eta'(0)$. Since $g(0) > 0$, $-\gamma\eta'(0) < 0$, we see that $E_1(0,0)$ is a hyperbolic saddle point. It is clear from (2.3) that on the y-axis, the flow is toward the origin and from the first equation of (2.3), we see that on the x-axis for small x, the flow is away from the origin (i.e. for small numbers of prey and predators, the prey population increases).

For $E_2(K,0)$, $M(x,y)$ reduces to

$$M(K,0) = \begin{bmatrix} Kg'(K) & -\xi'(0)p(K) \\ 0 & \eta'(0)(-\gamma + q(K)) \end{bmatrix} \tag{2.10}$$

We see that $M(K,0)$ has eigenvalues $Kg'(K)$ and $\eta'(0)(-\gamma + q(K))$. Since $g'(K) < 0$, $-\gamma + q(K) > 0$, $E_2(K,0)$ is again a hyperbolic saddle point. Clearly,

the flow near $(K,0)$ on the x-axis is toward $x = K$. There is a direction oblique to the x-axis (called the unstable manifold of $(K,0)$) in which the flow is away from $E_2(K,0)$.

Now, let us examine $E^*(x^*,y^*)$. $M(x,y)$ reduces to

$$M(x^*,y^*) = \begin{bmatrix} x^*g'(x^*) + g(x^*) - \xi(y^*)p'(x^*) & -\xi'(y^*)p(x^*) \\ \eta(y^*)q'(x^*) & 0 \end{bmatrix} \tag{2.11}$$

Denote $H(x^*) = x^*g'(x^*) + g(x^*) - \xi(y^*)p'(x^*)$. Since $\xi(y^*) = \frac{x^*g(x^*)}{p(x^*)}$, we can rewrite $H(x^*)$ as

$$H(x^*) = x^*g'(x^*) + g(x^*) - \frac{x^*g(x^*)}{p(x^*)}p'(x^*) \tag{2.12}$$

We note that $\det M(x^*,y^*) = \eta(y^*)q'(x^*)\xi'(y^*)p(x^*) > 0$. Hence the signs of the real parts of the eigenvalues of $M(x^*,y^*)$ coincide with the sign of $H(x^*)$. Therefore we have,

$$H(x^*) \begin{matrix} < 0 \\ > 0 \end{matrix} \Rightarrow E^*(x^*,y^*) \begin{matrix} \text{stable} \\ \text{unstable} \end{matrix} \tag{2.13}$$

The case where $H(x^*) = 0$ is a critical case in which $E^*(x^*,y^*)$ could be either a center or a stable spiral point or an unstable spiral point.

2.4 The method of Rosenzweig and MacArthur

There are several graphical techniques which have been developed to determine the stability of $E^*(x^*,y^*)$. Two of them are described in detail in Freedman (1980). Such techniques may be utilized to analyse the stability based on experimental data. We state here only one of them, namely, the method of Rosenzweig and MacArthur.

Before this description, we need to discuss the iscolines of system (2.3), which we now define.

Definition 2.1 The curve in the interior of the first quadrant of the $x-y$ plane along which the prey growth is instantaneously zero (i.e. $dx/dt = 0$) is called the prey isocline. The curve along which the predator growth is instantaneously zero is called the predator isocline.

For system (2.3), the predator isocline is trivial to graph. It is simply the vertical line $x = x^*$. The prey isocline is given by the graph of

$$\xi(y(x)) = \frac{xg(x)}{p(x)} \tag{2.14}$$

It is easy to see that the prey isocline passes through $(0, \xi^{-1}(\frac{g(0)}{p'(0)}))$, (x^*, y^*) and $(K, 0)$. Of course the intersection of the two isoclines is always at the equilibirum $E^*(x^*, y^*)$. If $\xi^{-1}(\frac{g(0)}{p'(0)}) \geq y^*$, this isocline may or may not have local maxima and/or minima. Otherwise, the prey isocline must have at least one local maximum. In Rosenzweig (1969), empirical ecological arguments are given to explain why the prey isocline should have at least one local maximum.

We now proceed to derive the results of Rosenzweig and MacArthur (1963). We consider again $H(x^*)$ as defined in (2.12) and note that since both x^* and $g(x^*)$ are positive, $\frac{H(x^*)}{x^* g(x^*)}$ has the same sign as $H(x^*)$. From (2.12), we have

$$\frac{H(x^*)}{x^* g(x^*)} = \frac{g'(x^*)}{g(x^*)} + \frac{1}{x^*} - \frac{p'(x^*)}{p(x^*)} = \frac{d}{dx} \ell n \left(\frac{xg(x)}{p(x)}\right) \Big|_{x=x^*} \tag{2.15}$$

Hence criterion (2.13) is equivalent to

$$\frac{d}{dx}\ell n\left(\frac{xg(x)}{p(x)}\right)\Big|_{x=x^*} \begin{matrix} <0 \\ >0 \end{matrix} \Rightarrow E^*(x^*,y^*) \begin{matrix} \text{stable} \\ \text{unstable} \end{matrix}. \tag{2.16}$$

However, the derivative of a function is positive or negative if and only if the function itself is increasing or decreasing respectively, and since the logarithm is an increasing function, (2.16) is equivalent to

$$\frac{xg(x)}{p(x)} \begin{matrix} \text{decreasing} \\ \text{increasing} \end{matrix} \text{ at } x^* \Rightarrow E^*(x^*,y^*) \begin{matrix} \text{stable} \\ \text{unstable} \end{matrix}. \tag{2.17}$$

This is the so called criterion of Rosenzweig and MacArthur (1963).

Looking at this criterion graphically, (2.17) implys that if the prey and predator isoclines intersect at a point of decrease of the prey isocline, the equilibrium is asymptotically stable. However, if the intersection is at a point of increase, the equilibrium is unstable.

2.5 Phase plane analysis, positive invariance and boundedness

We note that both the x-axis and the y-axis are invariant sets for system (2.3). Therefore the first quadrant $\{(x,y)|\, x \geq 0,\, y \geq 0\}$ is invariant also. In fact, the positive cone is invariant as well. This is proved in the following theorem.

THEOREM 2.1 (POSITIVE INVARIANCE). *Suppose* $(x(t),y(t))$ *is a solution of system (2.3) with* $x(0) = x_0 > 0$, $y(0) = y_0 > 0$. *Then* $x(t) > 0$, $y(t) > 0$ *for all* $t \in (-\infty,\infty)$.

Proof. Assume otherwise. Then there is a $T > 0$, such that $x(T)y(T) = 0$. Therefore either $x(T) = 0$ or $y(T) = 0$. If $x(T) = 0$, then the following initial value problem

$$\begin{aligned} \dot{x} &= xg(x) - \xi(y)p(x), \quad x(T) = 0 \\ \dot{y} &= \eta(y)(-\gamma + q(x)), \quad y(T) = y_T \geq 0 \end{aligned} \tag{2.18}$$

has a solution $(0, y(t))$ where $\dot{y}(t) = -\gamma\eta(y(t))$ and $y(T) = y_T \geq 0$. Since the solution of (2.18) is unique, it follows that $x(t) \equiv 0$ which contradicts the fact that $x(0) = x_0 > 0$. The case of $y(T) = 0$ can be proved similarly, completing the proof of the theorem.

In what follows we are going to carry out a detailed phase plane analysis of system (2.3) in the first quadrant. For convenience, we divide the first quadrant of the phase plane into five zones and their boundaries as described below:

$$\begin{aligned} \text{Zone I} &= \{(x,y) : x^* < x < K, \quad \xi(y) > \frac{xg(x)}{p(x)}\} \\ \text{Zone II} &= \{(x,y) : 0 < x < x^*, \quad \xi(y) > \frac{xg(x)}{p(x)}\} \\ \text{Zone III} &= \{(x,y) : 0 < x < x^*, \quad \xi(y) < \frac{xg(x)}{p(x)}\} \\ \text{Zone IV} &= \{(x,y) : x^* < x < K, \quad 0 < \xi(y) < \frac{xg(x)}{p(x)}\} \\ \text{Zone V} &= \{(x,y) : K \leq x, \quad 0 < y\} \end{aligned}$$

Note that the flow is across the prey isocline vertically, and across the predator isocline horizontally.

We analyse the phase plane by considering $\frac{dy}{dx}$, which has the following form

$$\frac{dy}{dx} = \frac{\eta(y)(-\gamma + q(x))}{xg(x) - \xi(y)p(x)} \tag{2.19}$$

We note that when $\xi(y) > \frac{xg(x)}{p(x)}$, on the predator isocline solutions cross from Zone I to Zone II, since $\frac{dx}{dt} < 0$, whereas when $\xi(y) < \frac{xg(x)}{p(x)}$, $\frac{dx}{dt} > 0$, and solutions cross from Zone III to Zone IV. When $0 < x < x^*$, $\frac{dy}{dt} < 0$ and hence solutions cross from Zone II to Zone III, and when $x^* < x < K$, $\frac{dy}{dt} > 0$, so that solutions cross from Zone IV to Zone I.

We now consider $\frac{dy}{dx}$ on the line $x = K$. Since $g(K) = 0$, (2.19) is reduced to

$$\frac{dy}{dx}|_{x=K} = \frac{\eta(y)(-\gamma + q(K))}{-\xi(y)p(K)} = -\frac{\eta(y)}{\xi(y)}\left(\frac{-\gamma + q(K)}{p(K)}\right) < 0. \qquad (2.20)$$

Also, $\frac{dx}{dt}|_{x=K} < 0$ if $y \neq 0$. Hence all solutions cross $x = K$ from Zone V to Zone I (see Fig. 2.1).

It is easy to see as well that $\frac{dy}{dx} < 0$ in Zones I and III, whereas $\frac{dy}{dx} > 0$ in Zones II and IV. Also $\frac{dy}{dx} < 0$ in Zone V. All of the above information gives us the flow pattern as illustrated in Fig. 2.1.

Now consider a solution initiating in Zone V. We note that $\frac{dy}{dt} = xg(x) - \xi(y)p(x) < 0$ since $g(x) \leq 0$ when $x \geq K$ and $|\frac{dx}{dt}| > \xi(y)p(K)$. Moreover, when $x \geq K$, $\frac{dy}{dt} = \eta(y)(-\gamma + q(x)) > 0$. Hence when $x(t) \geq K$, $y(t) > y(0) > 0$. Therefore $|\frac{dx(t)}{dt}| > \xi(y_0)p(K)$, whenever $x(t) \geq K$, which implies that all trajectories initiating in Zone V flow to the left and must cross $x = K$ into Zone I in finite time.

Consider now such a solution crossing $x = K$ into Zone I at $y = y_1$, where $y_1 > \max_{0 \leq x \leq K} \xi^{-1}(\frac{xg(x)}{p(x)})$. Let this trajectory be labeled Γ. Then Γ continues to

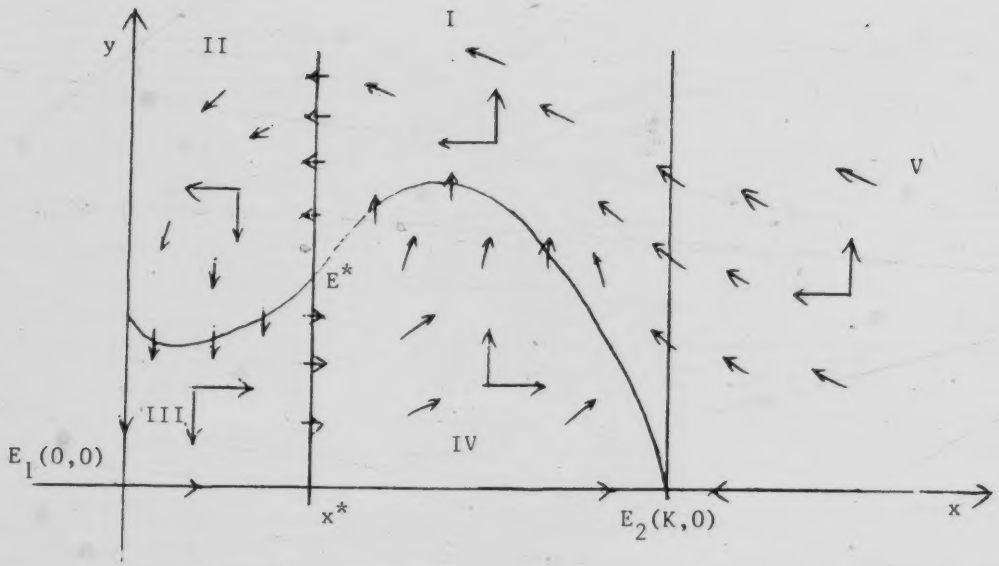

Figure 2.1 Flow direction in the phase plane for system (2.3).

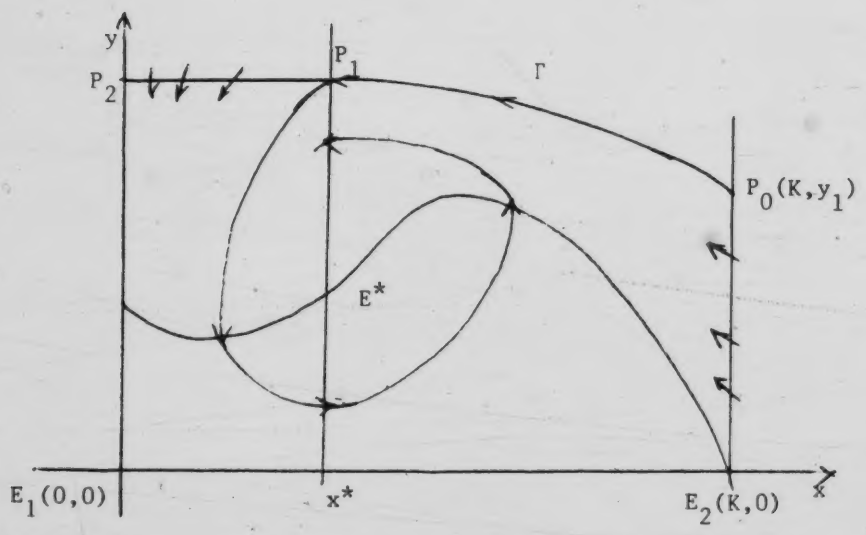

Figure 2.2. A positively invariant region for system (2.3).

the left with a negative slope. From (2.3), we see that $\frac{dy}{dt} = \eta(y)(-\gamma + q(x)) \geq 0$, when $x(t) \geq x^*$, and therefore

$$\frac{dx}{dt} = xg(x) - \xi(y)p(x) < xg(x) - \xi(y_1)p(x) < 0.$$

Let $0 > \alpha = \sup_{x^* \leq x \leq K} (xg(x) - \xi(y_1)p(x))$. Then $\frac{dx}{dt} < \alpha < 0$. Hence Γ must cross the predator isocline in finite time into Zone II. We denote the crossing point as $P_1 = (x^*, y(T)) = (x(T), y(T))$, where $(x(t), y(t))$ is the solution of (2.3) with $x(0) = K$, $y(0) = y_1$. Let $P_2 = (0, y(T))$, then the region bounded by the part of Γ from $P_0 = (K, y_1)$ to $P_1 = (x^*, y(T))$, the segment P_1P_2, P_2E_1, E_1E_2 and E_2P_0 is positively invariant. This implies that all the trajectories of system (2.3) will eventually enter this region, i.e. the system is dissipative, and hence all the solutions are bounded. Moreover, since both E_1 and E_2 are hyperbolic, we see that system (2.3) is uniformly persistent (see appendix F).

We note the omega limit set of Γ must be either the equilibrium $E^*(x^*, y^*)$ or a limit cycle. Which one of these is usually determined by the stability of $E^*(x^*, y^*)$. In any case, system (2.3) always has either a stable equilibrium or a stable from the outside limit cycle, or both.

2.6 Global asymptotic stability

The question of global stability in predator-prey systems is a very interesting mathematical problem. Many biologists believe that the unique positive locally asymptotically stable equilibrium in an ecological model is globally stable

in the positive cone. However, this is not always the case. By a similar technique as is utilized in Chapter IV of this thesis, we can see that it is easy to find a Gause-type predator-prey system with a unique locally asymptotically stable positive equilibrium which has at least one limit cycle surrounding it. Therefore, it is very important to find conditions which may guarantee the global stability of the unique positive equilibrium.

The global stability analysis for the classical Lotka-Volterra system has been given by Goh (1978). The method he used involved constructing a Lyapunov function. Hastings (1978) obtained a result more general than Goh's. Although Hastings' global stability result for predator-prey system is correct, his main result, Theorem 2, is not rigorously proven. Hsu et al (1978) employed the Dulac criterion (Poincaré's negative criterion) to prove global stability for a specific predator-prey model. In a subsequent paper, Hsu (1978) presented two criteria for global stability of a general predator-prey system of intermediate type.

For a special intermediate type of predator-prey system, where $\xi(y) = \eta(y) = y$, $q(x) = cp(x)$ for some constant c, $c > 0$, Cheng et al (1981) provided some interesting criteria for the global stability of the positive equilibrium. However, with some minor modification, their techniques can be extended and applied to system (2.3) to obtain similar results. In what follows, we just present the modified theorems. The detailed proofs will be omitted.

THEOREM 2.2. *For system (2.3), assume*

(1) : $\frac{d}{dx}\left(\frac{xq(x)}{p(x)}\right) < 0$, *for all* $x^* \leq x \leq K$,

(2) : $\frac{(2x^*-x)g(2x^*-x)}{p(2x^*-x)} \leq \frac{xg(x)}{p(x)}$ *for all* x,

(3) : $\frac{-\gamma+q(2x^*-x)}{p(2x^*-x)} < \frac{\gamma-q(x)}{p(x)}$ *for all* x, *such that* $x^* \leq x < \min\{2x^*, K\}$.

Then $E^*(x^*, y^*)$ *is globally asymptotically stable for system (2.3) with respect to the interior of the first quadrant.*

THEOREM 2.3. *For system (2.3), assume*

(1) : $E^*(x^*, y^*)$ *is locally asymptotically stable, i.e.* $f(x^*) < 0$, *where*

$$f(x) = \frac{d}{dx}(xg(x)) - \frac{p'(x)xg(x)}{p(x)} = p(x)\frac{d}{dx}(\frac{xg(x)}{p(x)})$$

(2) : $\frac{d}{dx}(\frac{f(x)-f(x^*)}{q(x)-q(x^*)}) \leq 0$ *for* $0 \leq x \leq K$.

Then $E^*(x^*, y^*)$ *is globally asymptotically stable in the interior of the first quadrant.*

THEOREM 2.4. *For system (2.3), assume* $E^*(x^*, y^*)$ *is locally asymptotically stable, and*

$$\frac{\eta(y^*)}{y^*}(-\gamma+q(x))(g(x)-\xi(y)\frac{p(x)}{x}) - \frac{\eta(y)}{y}(-\gamma+q(x))(g(x^*)-\xi(y)\frac{p(x^*)}{x^*}) \leq 0,$$

for $0 < x < K$, $y > 0$. *Then* $E^*(x^*, y^*)$ *is globally asymptotically stable in the interior of the first quadrant.*

In fact, Theorem 2.4 is similar to Theorem 4 of Cheng et al (1981), which is a corollary of their Theorem 3. This fact was overlooked by them and therefore their proof was not required. The same result will be proved in a remark of Chapter V in this thesis.

Similar to Hsu's (1978) results, we have the following

THEOREM 2.5. *If* $(\frac{xg(x)}{p(x)} - \xi(y)^*)(x-x^*) \leq 0$, *then* $E^*(x^*, y^*)$ *is globally asymptotically stable in the positive cone if and only if it is locally asymptotically stable.*

THEOREM 2.6. *Assume the equilibrium* $E^*(x^*, y^*)$ *of (2.3) is locally asymptotically stable. Further, the prey isocline is strictly concave down, i.e.* $\frac{d^2}{dx^2}(\frac{xg(x)}{p(x)}) < 0$, $0 \leq x \leq K$. *Then* $E^*(x^*, y^*)$ *is globally asymptotically stable in the positive cone.*

Remark: To use Hsu's proof for this theorem, the function $h(x, y)$ in Hsu's (1978) paper should be chosen differently, namely, $h(x, y) = \phi(x)/p(y)$, and $\phi(y)$ satisfies

$$\phi'(y) = \phi(y)(\frac{\beta - \eta'(y)}{\eta(y)}), \quad \phi(y^*) = 1 \qquad (*)$$

where β is a positive constant which satisfies (3.10) of Hsu's paper (1978).

Harrison (1979) considered an even more general model for a predator-prey interaction, namely

$$\begin{aligned} \dot{x} &= a(x) - f(x)b(y) \\ \dot{y} &= n(x)h(y) + c(y) \end{aligned} \qquad (2.21)$$

where $f(x)$, $n(x)$ and $b(y)$ are assumed nondecreasing functions, $f(x)$ and $h(y)$ are positive over an interval containing x^* and y^* respectively, and where (x^*, y^*) is the unqiue positive solution of

$$\begin{aligned} a(x) - f(x)b(y) &= 0 \\ n(x)h(y) + c(y) &= 0 \end{aligned} \qquad (2.22)$$

The following stability theorem for $E^*(x^*, y^*)$ was obtained by Harrison:

THEOREM 2.7. *Assume that* $(n(x) - n(x*))(x - x^*) > 0$ *for* $x \neq x^*$ *and* $(b(y) - b(y^*))(y - y^*) > 0$ *for* $y \neq y^*$, *and that, in a neighborhood of* $E^*(x^*, y^*)$, $a(x)/f(x)$ *and* $c(y)/h(y)$ *are both non-increasing with one of them strictly decreasing. Then the equilibrium point* $E^*(x^*, y^*)$ *is asymptotically stable. Let* x_L *and* y_L *be the smallest and* x_M *and* y_M *be the largest numbers, respectively, such that*

$$\begin{aligned} a(x) &\geq b(y^*)f(x) \quad \text{for } x_L < x < x^* \\ a(x) &\leq b(y^*)f(x) \quad \text{for } x^* < x < x_M \end{aligned} \tag{2.23}$$

$$\begin{aligned} c(y) &\geq -n(x^*)h(y) \quad \text{for } y_L < y < y^* \\ c(x) &\leq -n(x^*)h(y) \quad \text{for } y^* < y < y_M \end{aligned} \tag{2.24}$$

with the inequalities in either (2.23) or (2.24) being strict, according to whether $a(x)/f(x)$ *or* $c(y)/h(y)$ *is strictly decreasing. Let* $u = \min\{V(x_L, y^*), V(x_M, y^*), V(x^*, y_L), V(x^*, y_M)\}$ *where*

$$V(x, y) = \int_{x^*}^{x} \frac{n(s) - n(x^*)}{f(s)} ds + \int_{y^*}^{y} \frac{b(s) - b(y^*)}{h(s)} ds. \tag{2.25}$$

Then the domain of attraction of $E^*(x^*, y^*)$ *includes the set* $D_u = \{(x, y) : V(x, y) < u\}$.

Remark: If $x_L = 0$, $x_M = \infty$, $y_L = 0$, and $y_M = \infty$, then D_u is the entire positive cone. Therefore $E^*(x^*, y^*)$ is globally asymptotically stable in the positive cone. In this case, this theorem coincides with Theorem 2.5 for system (2.3), since $n(x^*) = -\gamma + q(x^*) = 0$, $a(x)/f(x) = xg(x)/p(x)$, and $b(y^*) = \xi(y^*)$.

Similar to the proof of Proposition 2 in Conway and Smoller (1986), we note that the following is valid.

THEOREM 2.8. *Assume $\xi(y), \eta(y), g(x), p(x)$ and $q(x)$ are fixed in system (2.3). If γ is chosen so that x^* is very close to K, then $E^*(x^*, y^*)$ is globally asymptotically stable over the positive cone.*

This fact was observed by G.S.K. Wolkowicz (1987) as well.

In the next chapter we prove a uniqueness result for limit cycle in system (2.3). In a similar manner we can prove the following global stability result for $E^*(x^*, y^*)$.

THEOREM 2.9. *Assume $E^*(x^*, y^*)$ is locally asymptotically stable, i.e $\frac{d}{dx}(\frac{xq(x)}{p(x)})|_{x=x^*} < 0$. Further, assume $\frac{d}{dx}\left(\frac{p(x)(\frac{xq(x)}{p(x)})'}{-\gamma+q(x)}\right) \geq 0$, for $0 < x < x^*$ and $x^* < x < K$. Then system (2.3) has no nontrivial periodic solutions and hence $E^*(x^*, y^*)$ is globally asymptotically stable over the positive cone.*

2.7 General theory of limit cycles in plane autonomous systems

Limit cycles of plane autonomous differential systems first appear in the classical paper of H. Poincaré (1881-1882). In the 1930's, van der Pol and A.A. Andronov showed that the closed orbit in the phase plane of a self-sustained oscillation occurring in a vacuum tube circuit is a limit cycle as considered by Poincaré. Since then, the existence, nonexistence, uniqueness, location and other properties of limit cycles have been studied extensively by mathematicians and

physicists. Since the 1950's, many mathematical models from physics, engineering, and chemistry, biology, economics, etc., were given as plane autonomous systems with limit cycles. Therefore, in the qualitative theory of differential equations, investigation of limit cycles is of great interest. However, it is also often difficult.

In the 1900, Hilbert set forth his famous list of problems (1901) at the International Congress of Mathematics. The second half of the sixteenth problem was, "what is the maximum number of limit cycles for the equation

$$\frac{dy}{dx} = \frac{Q_n(x,y)}{P_n(x,y)} \tag{2.26}$$

(P_n and Q_n are polynomials of real coefficients and degree not higher than n), and what are their relative positions?"

So far, most of the known results on the limit cycles of plane autonomous systems are for system of type (2.26) when $n = 2$. However, almost all the predator-prey models of biological interactions do not fall in that class. Therefore, only the general theory of limit cycles in plane autonomous systems may be applicable to predator-prey systems.

We consider the following system

$$\frac{dx}{dy} = P(x,y), \frac{dy}{dt} = Q(x,y) \tag{2.27}$$

where x, y and t are real variables, $P(x,y)$ and $Q(x,y)$ are continuous single-valued real functions of x, y, and uniqueness of its solution is guaranteed.

Definition 2.2 If the solution $x = \phi(t)$, $y = \psi(t)$ of system (2.27) is a nonconstant periodic function of t, then the locus of this solution in the (x, y) phase plane is a closed trajectory of (2.27). Any simple closed curve consisting of several equilibria and the trajectories which approach the equilibria as $t \to \pm\infty$ is called a singular closed trajectory of (2.27).

Definition 2.3 If system (2.27) has a solution $C^+ : x = x(t)$, $y = y(t)$ defined on a half-line $t \geq t_0$, its set $\Omega(C^+)$ of ω-limit points is the (possibly empty) set of points y_0 for which there exists a sequence $t_0 < t_1 < \cdots$, such that $t_n \to \infty$, and $y(t_n) \to y_0$ as $n \to \infty$. Correspondingly, if $C^- : x = x(t)$, $y = y(t)$ is defined for $t \leq t_0$, we define the set $A(C^-)$ of α-limit points and if $C : x = x(t)$, $y = y(t)$ is defined for $-\infty < t < \infty$, its set of limit points is defined to be $A(C) \cup \Omega(C)$.

Definition 2.4 An orbit $C_0 : x = x_0(t)$, $y = y_0(t)$ on a maximal interval (ω_-, ω_+) which is contained in some $\Omega(C^+)$, $C^+ \not\subset C_0$, is called an $(\omega-)$ limit orbit. If in addition $x = x_0(t)$, $y = y_0(t)$ is periodic, then C_0 is called an $(\omega-)$ limit cycle. (The condition $C^+ \not\subset C_0$ assures that not every periodic orbit C_0 is a limit cycle.)

THEOREM 2.10. *(Dulac). If there exists a continuously differentiable function $B(x, y)$ in a simply connected region G such that $\frac{\partial(BP)}{\partial x} + \frac{\partial(BQ)}{\partial y}$ has constant sign and is not identically zero in any subregion, then system (2.27) does not have any closed trajectory or singular closed trajectory lying entirely in G.*

Proof. Suppose (2.27) has a closed trajectory Γ (the other case being similar). Since G is simply connected, Γ and its interior lie entirely in G. From Green's formula we have

$$\oint_\Gamma BPdy - BQdx = \int\int_S (\frac{\partial(BP)}{\partial x} + \frac{\partial(BQ)}{\partial y})dxdy \tag{2.28}$$

where S is the union of Γ and its interior. Since $Pdy = Qdx$ holds everywhere along Γ, we see that the left side of (2.28) is zero, while the integrand on the right has constant sign but is not identically zero in S. This contradiction completes the proof.

There are various ways of establishing the existence of limit cycles. Examples are Hopf bifurcation theorem and the Poincaré-Bendixson theorem, the most common techniques utilized in the literature.

Suppose (2.27) has a closed trajectory Γ, negatively oriented, whose equations are

$$x = f(t), y = g(t) \tag{2.29}$$

where f and g are periodic functions of t with period T. Now introduce curvilinear coordinates (s, n) in a sufficiently small neighborhood of Γ, where s denotes the length on Γ, measured from a fixed point on Γ, positive in the clockwise direction, and n is the length of the normal of Γ, whose outward direction is taken as positive. Suppose the equations of Γ with s as parameter are

$$x = \phi(s), y = \psi(s). \tag{2.30}$$

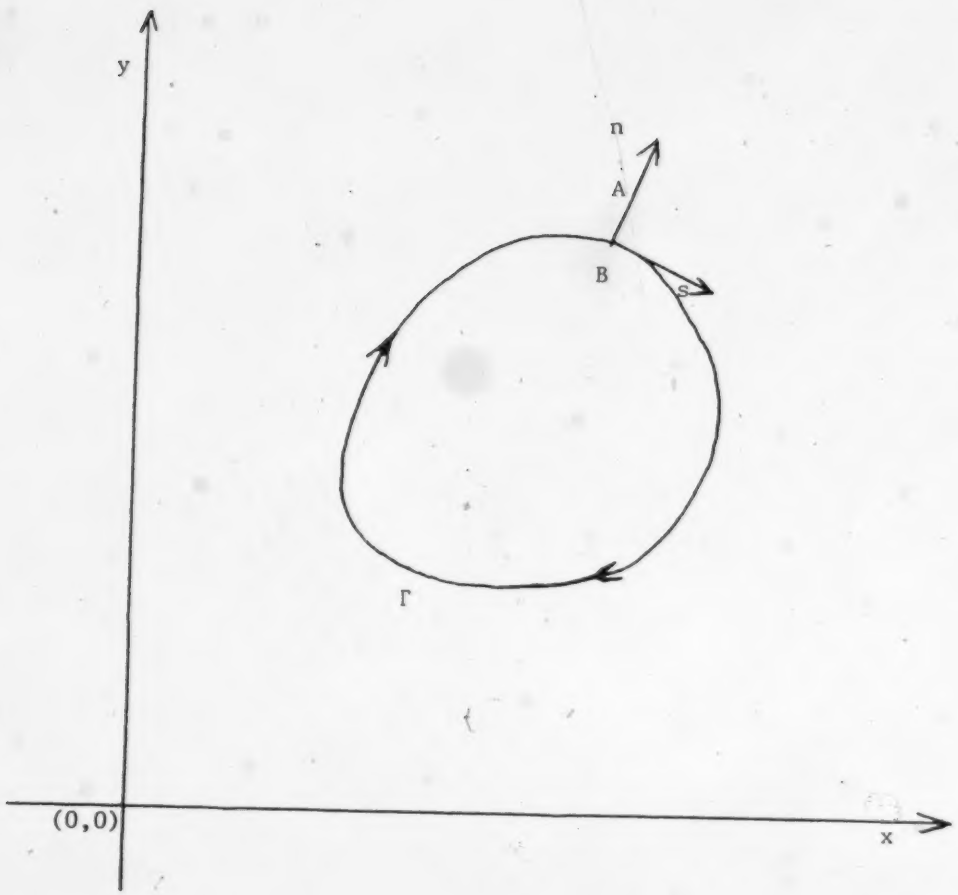

Figure 2.3 Rectangular coordinates and curvilinear coordinates.

For a point A in the vicinity of Γ, assume that A lies on the normal line of a point B on Γ (see Fig. 2.3).

Let the rectangular coordinates of B be $(\phi(s), \psi(s))$. Then the formula connecting the rectangular coordinates (x, y) of A and its curvilinear coordinates (s, n) is

$$x = \phi(s) - n\psi'(s),\ y = \psi(s) + n\phi'(s) \tag{2.31}$$

where

$$\phi'(s) = \frac{dx}{ds}\Big|_B = \frac{P_0}{\sqrt{P_0^2 + Q_0^2}},\quad \psi'(s) = \frac{dy}{ds}\Big|_B = \frac{Q_0}{\sqrt{P_0^2 + Q_0^2}} \tag{2.32}$$

where

$$P_0 = P(\phi(s), \psi(s)),\quad Q_0 = Q(\phi(s), \psi(s)).$$

substituting from (2.31) into (2.27), we obtain

$$\frac{dy}{dx} = \frac{\psi'(s) + \phi'(s)(\frac{dn}{ds}) + n\phi''(s)}{\phi'(s) - \psi'(s)(\frac{dn}{ds}) - n\phi''(s)} = \frac{Q(\phi(s) - n\psi'(s), \psi(s) + n\phi'(s))}{P(\phi(s) - n\psi'(s), \psi(s) + n\phi'(s))},$$

from which, we have

$$\frac{dn}{ds} = \frac{Q\phi' - P\psi' - n(P\phi'' + Q\psi'')}{P\phi' + Q\psi'} = F(s, n) \tag{2.33}$$

We observe that equation (2.33) has a zero solution, $n = 0$, which corresponds to the periodic trajectory Γ. When both $P, Q \in C^k$, $F(s, n)$ also belongs to C^k with respect to n. Assume $n(s, n_0)$ is a solution of (2.33), where $n(0) = n_0 > 0$ is very small. Then $n(T, n_0)$ as a function of n_0 also belongs to C^k. If both P and Q are analytic functions, then so is $n(T, n_0)$. Assume $n(T, n_0) \not\equiv n_0$ in a sufficiently small neighborhood of n_0 near $n_0 = 0$, then there

are only finitely many solutions to $n(T, n_0) = n_0$ by the analyticity of $n(T, n_0)$. Since there is a one to one correspondence between the solutions of $n(T, n_0) = n_0$ and the periodic solution of (2.27), we obtain the following result.

THEOREM 2.11. *If P, Q are analytic functions and system (2.27) is dissipative, and has only a finite number of equilibria, none of which is a center, and all stable and unstable manifolds intersect transversally, then system (2.27) has only a finite number of limit cycles in R^2.*

Assuming $P, Q \in C^1$, then (2.33) can be written as

$$\frac{dn}{ds} = F_n'(s,n)|_{n=0} \cdot n + o(n). \tag{2.34}$$

In order to compute $F_n'(s,n)|_{n=0}$, we note that

$$\begin{aligned} \phi'' &= -\frac{Q_0}{(P_0^2+Q_0^2)^2}[P_0^2 Q_{x_0} + P_0 Q_0 (Q_{y_0} - P_{x_0}) - Q_0^2 P_{y_0}] \\ \psi'' &= -\frac{P_0}{(P_0^2+Q_0^2)^2}[P_0^2 Q_{x_0} + P_0 Q_0 (Q_{y_0} - P_{x_0}) - Q_0^2 P_{y_0}] \end{aligned} \tag{2.35}$$

where P_{y_0}, P_{x_0}, Q_{y_0} and Q_{x_0} denote the value of the partial derivatives of P and Q at $n = 0$. Denoting $P = P_0$, $Q = Q_0$, and in view of the fact that $P_0\phi'' + Q_0\psi'' = 0$, we can obtain

$$F_n'(s,n)|_{n=0} = \frac{P_0^2 Q_{y_0} - P_0 Q_0 (P_{y_0} + Q_{x_0}) + Q_0^2 P_{x_0}}{(P_0^2+Q_0^2)^{3/2}} = H(s). \tag{2.36}$$

Hence the linear approximation equation of (2.33) is

$$\frac{dn}{ds} = H(s)n \tag{2.37}$$

whose solution is

$$n = n_0 \exp\left(\int_0^s H(s')ds'\right) \tag{2.38}$$

where $n_0 = n(0)$. Let the arc length of Γ be ℓ, denoting $ds = \sqrt{P_0^2 + Q_0^2}dt$, we have

$$\begin{aligned}\int_0^\ell H(s)ds &= \int_0^T \frac{1}{P_0^2+Q_0^2}[P_0^2 Q_{y_0} - P_0 Q_0(P_{y_0} + Q_{x_0}) + Q_0^2 P_{x_0}]dt \\ &= \int_0^T (P_{x_0} + Q_{y_0})dt - \frac{1}{2}\oint_\Gamma \frac{d(P_0^2+Q_0^2)}{P_0^2+Q_0^2} \\ &= \int_0^T (P_{x_0} + P_{y_0})dt = \int_0^T (\frac{\partial P}{\partial x} + \frac{\partial P}{\partial y})dt\end{aligned}$$

Thus we obtain the following well known result.

THEOREM 2.12. *If on a closed trajectory Γ of system (2.27)*

$$\int_0^T (\frac{\partial P}{\partial x} + \frac{\partial Q}{\partial y})dt < 0 \quad (> 0) \tag{2.39}$$

then Γ is a stable (unstable) limit cycle.

For predator-prey system (2.3), the functions $g(x), \xi(y), p(x), \eta(y)$ and $q(x)$ tend to be chosen as analytical functions in specific models, in which case system (2.3) has at most a finite number of limit cycles, by Theorem 2.11. Furthermore, by assuming the unique positive equilibrium $E^*(x^*, y^*)$ to be unstable, we have the following theorem.

THEOREM 2.13. *Suppose $E^*(x^*, y^*)$ in system (2.3) is unstable and $g(x), \xi(y)$, $p(x), \eta(y), q(x)$ are analytic, then (2.3) has at most a finite number of limit cycles and at least one asymptotically stable limit cycle.*

For results concerning the structural stability of system (2.27) and its limit cycles, see Erle (1979) and Ye et al (1986).

CHAPTER III

UNIQUENESS OF LIMIT CYCLES IN GAUSE-TYPE PREDATOR-PREY SYSTEMS

3.1 Introduction

Since the papers of May (1972) and Albrecht, Gatzke and Wax (1973), an outstanding problem in mathematical modeling of ecological systems has been that of determining conditions which guarantee uniqueness of limit cycles in predator-prey models.

In two dimensions it is well known that there can be no limit cycles in models of competitive or cooperative systems. Further, it is well known for predator-prey systems that the existence and stability of a limit cycle is related to the existence and stability of a positive equilibrium.

We assume such a positive equilibrium exists, for otherwise the predator population tends to extinction (see section 2.3, or Chapter 4 of Freedman (1980)). If the equilibrium is asymptotically stable, there may exist limit cycles, the innermost of which must be unstable from the inside, and the outermost of which must be stable from the outside. If limit cycles do not exist in this case, the equilibrium is globally asymptotically stable. Conditions for this last situation to occur are discussed briefly in section 2.6 of this thesis.

There are various techniques for establishing the existence of limit cycles (see section 2.7). However, we emphasize that criteria for their uniqueness are virtually unknown.

If the positive equilibrium exists and is unstable, there must occur at least one limit cycle. In 1972, May claimed that under the Kolmogorov conditions, a "unique", stable limit cycle must exist. In response to this, Albrecht et al (1973) constructed a predator-prey system satisfying the Kolmogorov conditions (except for the self contradictions contained therein) for which there are uncountably many periodic solutions filling an annular region between two limit cycles.

In 1981, Cheng published a result giving criteria for the uniqueness of limit cycles when they exist for a specialized class of predator-prey models. Subsequently, Liou and Cheng (1987) have corrected a flaw in the proof of Cheng's (1981) main theorem and extended the class of predator-prey models for which the results are valid.

In this chapter, by a different technique, we are able to obtain criteria for uniqueness of limit cycles in the case of an unstable positive equilibrium for the more general class of Gause-type predator-prey systems, which include those studied by Liou and Cheng as a special case, and which allow for the possibility of mutual interference among predators. The technique we use is to transform our model to a generalized Liénard system as studied by Cherkas et al (1970) and Zhang (1986). We note that aside from the usual predator-prey assumptions, one additional assumption is required for the uniqueness of limit cycles.

In the next section, we describe briefly the uniqueness result of Liou and Cheng. In section 3.3, we describe the generalized Liénard system and results

on the uniqueness of limit cycles of the system. Section 3.4 describes our tranformations and main theorems. This is followed by a section giving examples to illustrate our results. The final section contains a discussion. We complete the proof of a required theorem of Cherkas and Zhilevich (1970) in the appendix of this chapter.

3.2 Liou and Cheng's uniqueness result

The predator-prey system considered by Liou and Cheng takes the form

$$\begin{aligned} \dot{x} &= x(f(x) - y) \quad x(0) = x_0 > 0 \\ \dot{y} &= y(g(x) - \lambda) \quad y(0) = y_0 > 0. \end{aligned} \tag{3.1}$$

The general assumptions about $f(x)$ and $g(x)$ are:

(1) $g(x) \in C^1([0,\infty))$, $g(0) = 0$, $g'(x) > 0$ for all $x \geq 0$.

(2) $f(x) \in C^2([0,\infty))$, $f(0) \geq 0$ and there exists $K > 0$, such that $(x - K)f(x) < 0$ for $x \neq K$. There exists an α, $0 < \alpha < K$, such that $f'(x) > 0$ for $0 < x < \alpha$, $f'(\alpha) = 0$ and $f'(x) < 0$ for $x > \alpha$.

(3) There exists x^*, $0 < x^* < \alpha$, $g(x^*) = \lambda$, $y^* = f(x^*)$.

(4) $\frac{d}{dx}(\frac{xf'(x)}{g(x)-\lambda}) < 0$ for $x < x^*$ and $x > \overline{x}^*$, where $\overline{x}^* = f_2^{-1} \circ f_1(x^*)$, and $f_1 = f|_{(0,\alpha)}$, $f_2 = f|_{(\alpha,K)}$.

By the same method as utilized in Cheng (1981), they proved the following theorem:

THEOREM 3.1. *(Liou and Cheng). Under the assumptions (1)-(4), system (3.1) possesses a unique limit cycle which is globally stable.*

To obtain the above theorem, the assumptions made for $f(x)$ are crucial and essential in their proof. Obviously, the Gause-type predator-prey system is more general than (3.1).

For the proof of Theorem 3.1, see Liou and Cheng (1988), or consult Cheng (1981).

3.3 Results on a Generalized Liénard System

The following theorem was proved by L.A. Cherkas and L.I. Zhilevich in 1969. Since complete details of the proof were not given in the original paper, and since we require a different format we have included its proof in the appendix of this chapter.

THEOREM 3.2. *(L.A. Cherkas and L.I. Zhilevich). Let the generalized Lienard system*

$$\begin{aligned} \frac{dx}{dt} &= -(\varphi(y) + F(x)) \\ \frac{dy}{dt} &= h(x) \end{aligned} \tag{3.2}$$

satisfy the following conditions:

(1) $xh(x) > 0$ *when* $x \neq 0$ *and* $y\varphi(y) > 0$ *when* $y \neq 0$.

(2) $\varphi(y)$ *is monotonically increasing,* $F(0) = 0$, *and* $f(0) < 0$ (> 0), *where* $f(x) = F'(x)$.

(3) There exist real numbers α *and* β *such that the function*

$$f_1(x) = f(x) + h(x)(\alpha + \beta F(x)) \tag{3.3}$$

has simple zeros $x_1 < 0$ *and* $x_2 > 0$, *and* $f_1(x) \leq 0$ (≥ 0) *in* $x_1 < x < x_2$.

(4) Outside $x_1 \leq x \leq x_2$ *the function* $f_1(x)/h(x)$ *does not decrease (does not increase).*

(5) All the limit cycles contain the interval $x_1 \leq x \leq x_2$ *on the* x *axis.*

Then the system (3.2) has at most one limit cycle, which, if it exists, is stable (unstable).

From the proof of this theorem (see the appendix) we observe that condition 4 can be modified to

(4') *All the limit cycles are contained in the interval* $x_3 \leq x \leq x_4$, *where*

$$x_3 < x_1 < 0 < x_2 < x_4$$

and the function $\frac{f_1(x)}{h(x)}$ *does not decrease (does not increase) in* $x_3 \leq x \leq x_1$ *and* $x_2 \leq x \leq x_4$.

In the case $\beta = 0$ and $f_1(x)/h(x)$ does not decrease when x increases in $(-\infty, 0)$ and $(0, \infty)$, Theorem 3.2 reduces to Z.-F. Zhang's uniqueness theorem. However, some modifications can be made to her original theorem. Here we state only the modified theorem which can be viewed as a corollary of Theorem 3.2.

THEOREM 3.3. *(Modified Zhang's theorem) Consider the system (3.2). Suppose the following conditions are satisfied:*

(1) $xh(x) > 0$, *when* $x \neq 0$, $y\varphi(y) > 0$, *when* $y \neq 0$.

(2) $\varphi(y)$ *is nondecreasing, and the curve* $\varphi(y) + F(x) = 0$ *is defined for all* $x \in (-\infty, +\infty)$.

(3) $F(0) = 0$, $f(0) < 0$, *where* $f(x) = F'(x)$.

(4) All limit cycles are contained in the interval $a < x < b$ *where* $a < 0 < b$ *and* $f(x)/h(x)$ *is nondecreasing when* x *increases in* $a < x < 0$ *and* $0 < x < b$.

Then system (3.2) has at most one limit cycle, and, if it exists, it is asymptotically stable.

3.4. Transformations and Main Results

We consider the Gause-type predator-prey system

$$\begin{aligned} \dot{x} &= xg(x) - \xi(y)p(x) \\ \dot{y} &= \eta(y)(-\gamma + q(x)) \\ x(0) &= x_0 \geq 0,\ y(0) = y_0 \geq 0 \end{aligned} \tag{3.4}$$

As in section 2.2 and 2.3, we assume (H1) to (H7) for (3.4). Further, we assume the unique positive equilibrium to be unstable, which is equivalent to

(H8) $\frac{d}{dx}\left(\frac{xq(x)}{p(x)}\right)\Big|_{x=x^*} > 0$

according to the method of Rosenzweig and MacArthur.

Our main results, Theorems 3.4 and 3.5 are obtained by transforming system (3.4) to a generalized Liénard system of type (3.2).

First, let

$$\begin{aligned} X &= x - x^* \\ Y &= y - y^*. \end{aligned} \tag{3.5}$$

By substituting (3.5) into (3.4), we obtain

$$\begin{aligned} \dot{X} &= (X + x^*)g(X + x^*) - \xi(Y + y^*)p(X + x^*) \\ \dot{Y} &= \eta(Y + y^*)(-\gamma + q(X + x^*)). \end{aligned} \tag{3.6}$$

Hence we have

$$\frac{d}{dt}\Big(\int_0^Y \frac{ds}{\eta(s+y^*)}\Big) = -\gamma + q(X+x^*)$$

and

$$\frac{d}{dt}\Big(\int_0^X \frac{ds}{p(s+x^*)}\Big) = (X+x^*)\frac{g(X+x^*)}{p(X+x^*)} - \xi(Y+y^*). \tag{3.7}$$

Now let

$$\begin{aligned} u &= \int_0^X \frac{ds}{p(s+x^*)} = k(X) \\ v &= \int_0^Y \frac{ds}{\eta(s+y^*)} = \ell(Y). \end{aligned} \tag{3.8}$$

Hence

$$X = k^{-1}(u), \qquad Y = \ell^{-1}(v). \tag{3.9}$$

Further

$$\begin{aligned} \dot{u} &= (k^{-1}(u)+x^*)\frac{g(k^{-1}(u)+x^*)}{p(k^{-1}(u)+x^*)} - \xi(\ell^{-1}(v)+y^*) \\ \dot{v} &= -\gamma + q(k^{-1}(u)+x^*). \end{aligned} \tag{3.10}$$

It is easy to see $\frac{dk}{du} > 0$, $\frac{d\ell}{dv} > 0$, $\frac{dk^{-1}}{du} > 0$ and $\frac{d\ell^{-1}}{dv} > 0$.

Now, we rewrite (3.10) as follows

$$\begin{aligned} \dot{u} &= -\Big(\xi(y^*) - (k^{-1}(u)+x^*)\frac{g(k^{-1}(u)+x^*)}{p(k^{-1}(u)+x^*)}\Big) - (\xi(\ell^{-1}(v)+y^*) - \xi(y^*)) \\ \dot{v} &= -\gamma + q(k^{-1}(u)+x^*). \end{aligned} \tag{3.11}$$

By comparing (3.11) with (3.2), we have the following correspondences:

$$h(x) \leftrightarrow -\gamma + q(k^{-1}(u)+x^*)$$

$$\varphi(y) \leftrightarrow \xi(\ell^{-1}(v)+y^*) - \xi(y^*)$$

$$F(x) \leftrightarrow \xi(y^*) - (k^{-1}(u)+x^*)\frac{g(k^{-1}(u)+x^*)}{p(k^{-1}(u)+x^*)}.$$

Hence, if we define

$$h(u) = -\gamma + q(k^{-1}(u) + x^*)$$

$$\varphi(v) = \xi(\ell^{-1}(v) + y^*) - \xi(y^*) \tag{3.12}$$

$$F(u) = \xi(y^*) - (k^{-1}(u) + x^*)\frac{g(k^{-1}(u) + x^*)}{p(k^{-1}(u) + x^*)},$$

we may observe that the following hold

1. $h(0) = -\gamma + q(x^*) = 0$; $h'(u) > 0$, hence $uh(u) > 0$ when $u \neq 0$. Similarly, $v\varphi(v) > 0$, when $v \neq 0$.
2. $\varphi'(v) = \frac{d\xi(\ell^{-1}(v)+y^*)}{d(\ell^{-1}(v)+y^*)} \cdot \frac{d\ell^{-1}(v)}{dv} > 0$, i.e., $\varphi(v)$ is monotonically increasing.
3. $\varphi(v) + F(u) = 0$ is defined for all $u \in (-\infty, +\infty)$.
4. $\frac{dF(0)}{du} = \frac{dF(u)}{d(k^{-1}(u)+x^*)} \cdot \frac{d(k^{-1}(u)+x^*)}{du}\Big|_{u=0} < 0$ from H8, and the fact that $\frac{dk^{-1}(0)}{du} > 0$.
5. For such models, it is known [Freedman (1980), Ch. 4] that the limit cycles of (3.4) must lie inside the strip $0 < x < K$, $0 < y < \infty$. Hence the limit cycles of (3.11) must lie inside the strip $-\infty < u < k(K)$, $-\infty < v < +\infty$.
6. $$f(u) = F'(u) = \frac{dF(u)}{d(k^{-1}(u) + x^*)} \frac{dk^{-1}(u)}{du}. \tag{3.13}$$

Since system (3.4) has a unique limit cycle if and only if system (3.11) has a unique limit cycle, we have the following general theorems.

Corresponding to Theorem 3.2, we obtain

THEOREM 3.4. *In system (3.11), suppose there exist real numbers α and β, such that*

$$f_1(u) = f(u) + h(u)[\alpha + \beta F(u)]$$

has simple zeros $u_1 < 0 < u_2$, and $f_1(u) \le 0$ in $u_1 \le u \le u_2$, and the function $f_1(u)/h(u)$ is nondecreasing in $(-\infty, u_1)$, $(u_2, k(K))$. Moreover, suppose all the limit cycles contain the interval $u_1 \le u \le u_2$ on the u-axis. Then system (3.4) has exactly one limit cycle which is globally asymptotically stable with respect to the set $\{(x,y) \mid x > 0,\ y > 0\}\backslash\{E^*\}$.

Corresponding to Theorem 3.3, we obtain

THEOREM 3.5. *Suppose in system (3.11) $\frac{f(u)}{h(u)}$ is nondecreasing in $(-\infty, 0)$ and $(0, k(K))$. Then system (3.4) has exactly one limit cycle which is globally asymptotically stable with respect to the set $\{(x,y) \mid x > 0,\ y > 0\}\backslash\{E^*\}$.*

In most systems discussed in the ecological literature, $\xi(y) = \eta(y) = y$. In this case, we have the following simplifications.

$$u = k(X), \qquad v = \ell(Y) = \ln \frac{Y + y^*}{y^*} \tag{3.14}$$

or

$$Y = y^* e^v - y^*. \tag{3.15}$$

Hence (3.11) can be rewritten as

$$\begin{aligned} \dot{u} &= -\Big(y^* - (k^{-1}(u) + x^*)\frac{g(k^{-1}(u) + x^*)}{p(k^{-1}(u) + x^*)}\Big) - (y^* e^v - y^*) \\ \dot{v} &= -\gamma + q(k^{-1}(u) + x^*). \end{aligned} \tag{3.16}$$

Note that

$$u = \int_0^X \frac{ds}{p(s+x^*)} = k(X); \qquad X = k^{-1}(u).$$

Hence

$$\begin{aligned} \frac{du}{dX} &= \frac{1}{p(X+x^*)}, \quad \text{or} \\ \frac{dk^{-1}(u)}{du} &= \frac{dX}{du} = p(X+x^*) = p(k^{-1}(u)+x^*), \end{aligned} \tag{3.17}$$

and

$$\begin{aligned} f(u) &= \frac{dF(u)}{d(k^{-1}(u)+x^*)} \cdot p(k^{-1}(u)+x^*) \\ &= -(xg'(x)+g(x)-xg(x)\frac{p'(x)}{p(x)})\Big|_{x=k^{-1}(u)+x^*} . \end{aligned} \tag{3.18}$$

Assuming $\frac{f(u)}{h(u)}$ is differentiable, then $\frac{f(u)}{h(u)}$ is nondecreasing if and only if $\frac{d}{du}\left(\frac{f(u)}{h(u)}\right) \geq 0$. Since

$$\frac{d}{du}\Big(\frac{f(u)}{h(u)}\Big) = \frac{d}{d(k^{-1}(u)+x^*)}\Big(\frac{f(k^{-1}(u)+x^*)}{h(k^{-1}(u)+x^*)}\Big) \cdot p(k^{-1}(u)+x^*),$$

$\frac{f(u)}{h(u)}$ is nondecreasing if and only if

$$-\frac{d}{dx}\Big(\frac{xg'(x)+g(x)-xg(x)\frac{p'(x)}{p(x)}}{-\gamma+q(x)}\Big) \geq 0. \tag{3.19}$$

It is clear that the above computation of $\frac{d}{du}\left(\frac{f(u)}{h(u)}\right)$ has nothing to do with $\xi(y)$ and $\eta(y)$. Therefore, we have the following version of Theorem 3.5 for system (3.4).

THEOREM 3.6. *Suppose in system (3.4)*

$$\frac{d}{dx}\Big(\frac{xg'(x)+g(x)-xg(x)\frac{p'(x)}{p(x)}}{-\gamma+q(x)}\Big)\le 0 \tag{3.20}$$

in $0\le x<x^*$ *and* $x^*<x\le K$. *Then system (3.4) has exactly one limit cycle which is globally asymptotically stable with respect to the set* $\{(x,y)\mid x>0,\ y>0\}\backslash\{E^*\}$.

Remark: Clearly (3.20) is equivalent to $\frac{d}{dx}\Big(\frac{p(x)(\frac{xg(x)}{p(x)})'}{-\gamma+q(x)}\Big)\le 0$. In the case $q(x)=cp(x)$, (3.20) is equivalent to

$$\begin{aligned}0&\ge \frac{d}{dx}\Big(\frac{xg'(x)+g(x)-xg(x)\frac{p'(x)}{p(x)}}{-\gamma+cp(x)}\Big)\\ &=\frac{\big(p(x)(\frac{xg(x)}{p(x)})''+p'(x)(\frac{xg(x)}{p(x)})'\big)\big(-\gamma+cp(x)\big)-cp'(x)p(x)(\frac{xg(x)}{p(x)})'}{(-\gamma+cp(x))^2}\\ &=\frac{(cp(x)-\gamma)p(x)(\frac{xg(x)}{p(x)})''-\gamma p'(x)(\frac{xg(x)}{p(x)})'}{(-\gamma+cp(x))^2}\end{aligned}$$

i.e.,

$$(cp(x)-\gamma)p(x)\Big(\frac{xg(x)}{p(x)}\Big)''-\gamma p'(x)\Big(\frac{xg(x)}{p(x)}\Big)'\le 0. \tag{3.21}$$

Furthermore, if $p(x)=\alpha x$, then (3.21) can be simplified as

$$(c\alpha x-\gamma)xg''(x)-\gamma g'(x)\le 0 \tag{3.22}$$

while (3.20) is equivalent to

$$\frac{d}{dx}\Big(\frac{xg'(x)}{-\gamma+c\alpha x}\Big)\le 0. \tag{3.23}$$

In case $p(x)=\alpha x$ and for arbitrary $q(x)$, (3.20) is reduced to

$$\frac{d}{dx}\Big(\frac{xg(x)}{-\gamma+q(x)}\Big)\le 0 \tag{3.24}$$

which is very similar to the condition (4) in Liou and Cheng's result. In Chapter V of this thesis, we will point out some further improvements of these results.

3.5 Examples

Example 1. We first consider the system

$$\begin{aligned} \dot{s}(t) &= rs(t)\Big(1-\frac{s(t)}{K}\Big)-\Big(\frac{m}{\alpha}\Big)\Big(\frac{y(t)s(t)}{a+s(t)}\Big), \\ \dot{y}(t) &= y(t)\Big(\frac{ms(t)}{a+s(t)}-D_0\Big), \qquad s(0)=s_0>0, \quad y(0)=y_0>0 \end{aligned} \tag{3.25}$$

discussed in Waltman (1983), where r, k, m, α, a, D_0 are positive constants. The following results are known (see Waltman, 1983).

1. Solutions of (3.25) are positive and eventually uniformly bounded.

Denote $\lambda = \frac{a}{(\frac{m}{D_0})-1}$ if $m > D_0$.

(a) If $m \le D_0$, or if $m > D_0$ and $K \le \lambda$, then the equilibrium $E_1(K,0)$ is asymptotically stable and $\lim\limits_{t\to\infty} s(t) = K$, $\lim\limits_{t\to\infty} y(t) = 0$.

(b) If $\lambda < K \le a+2\lambda$, the equilibrium $E^*(\lambda, y^*)$ is asymptotically stable, and $\lim_{t\to\infty} s(t) = \lambda$, $\lim_{t\to\infty} y(t) = y^*$, where $y^* = \frac{r\alpha}{m}\big(1-\frac{\lambda}{K}\big)(a+\lambda)$.

(c) If $K > a+2\lambda$, then (λ, y^*) is unstable and there exists at least one periodic orbit in the first quadrant of the $s-y$ plane.

By using a symmetry argument, Cheng (1981) proved that if $K > a+2\lambda$, then system (3.25) possesses a unique limit cycle which is stable. The proof is very tedious. However, by employing Theorem 3.6, this result can be obtained easily. This will be equivalent to proving the following.

$$\frac{d}{ds}\Big[\frac{\big(r\big(1-\frac{s}{K}\big)+s\big(-\frac{r}{K}\big)\big)\frac{m}{\alpha}\frac{s}{a+s}-s\frac{a}{a+s}\frac{m}{\alpha}r\big(1-\frac{s}{K}\big)}{\frac{m}{\alpha}\frac{s}{a+s}\big(\frac{ms}{a+s}-D_0\big)}\Big] \le 0 \tag{3.26}$$

$$\Leftrightarrow \frac{d}{ds}\left[\frac{r\left(1-\frac{s}{K}\right)+s\left(-\frac{r}{K}\right)-\frac{ar}{a+s}\left(1-\frac{s}{K}\right)}{\frac{ms}{a+s}-D_0}\right] \leq 0$$

$$\Leftrightarrow \frac{d}{ds}\left[\frac{s\left(-\frac{r}{K}\right)+\frac{s}{a+s}\,r\left(1-\frac{s}{K}\right)}{\frac{ms}{a+s}-D_0}\right] \leq 0$$

$$\Leftrightarrow \frac{d}{ds}\left[\frac{rs(a+s)+rs(s-K)}{ms-D_0(a+s)}\right] \geq 0$$

$$\Leftrightarrow \frac{d}{ds}\left[\frac{r}{m-D_0}\,\frac{s(2s+a-K)}{s-\lambda}\right] \geq 0$$

$$\Leftrightarrow \frac{d}{ds}\left(\frac{s(2s+a-K)}{s-\lambda}\right) \geq 0$$

$$\Leftrightarrow (2s+a-K+2s)(s-\lambda)-s(2s+a-K) \geq 0$$

$$\Leftrightarrow 2s^2-4\lambda s-\lambda(a-K) \geq 0$$

$$\Leftrightarrow s^2-2\lambda s+\lambda\left(\frac{K-a}{2}\right) \geq 0$$

$$\Leftrightarrow (s-\lambda)^2+\lambda\left(\frac{K-a}{2}\right)-\lambda^2 \geq 0$$

$$\Leftrightarrow \frac{K-a}{2} \geq \lambda$$

i.e., $K \geq a+2\lambda$.

The equality holds if and only if $K = a+2\lambda$. This completes the proof of uniqueness in case (c).

Example 2. We consider the more general model

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1-\left(\frac{x}{K}\right)^{\theta}\right)-y\left(\frac{\alpha x}{a+x}\right)^{m}\\ \frac{dy}{dt} &= y\left(-\gamma+\beta\left(\frac{\alpha x}{a+x}\right)^{m}\right),\end{aligned} \tag{3.27}$$

where r, γ, α, β, a, m, $\theta > 0$. In the following calculation, we set $\theta = 2$, $m = 1$. Hence

$$g(x) = r\left(1-\left(\frac{x}{K}\right)^2\right), \qquad p(x) = \frac{\alpha x}{a+x}, \qquad q(x) = \beta p(x).$$

Suppose $(\bar{x}, \bar{y})$ is the unique positive equilibrium of (3.27). Then $\frac{\gamma}{\beta} = \frac{\alpha \bar{x}}{a+\bar{x}}$ or $\bar{x} = \frac{a\gamma}{\alpha\beta-\gamma} \equiv \lambda > 0 \Leftrightarrow \alpha\beta > \gamma$. Hence we assume $\alpha\beta > \gamma$ and $\lambda < K$ which implies $\bar{y} = \frac{\beta}{\gamma} \cdot r\lambda\big(1 - \big(\frac{\lambda}{K}\big)^2\big)$.

By the Rosenzweig–MacArthur criterion, to ensure $(\bar{x}, \bar{y})$ is unstable we need

$$r x\big(1 - \big(\frac{x}{K}\big)^2\big)\frac{a+x}{\alpha x} = \frac{r}{\alpha}(a+x)\big(1 - \big(\frac{x}{K}\big)^2\big)$$

should be increasing at $(\bar{x}, \bar{y})$, i.e.,

$$\frac{r}{\alpha}\big(1 - \big(\frac{\lambda}{K}\big)^2\big) + \frac{r}{\alpha}(a+\lambda)\big(-\frac{2\lambda}{K^2}\big) > 0$$

or

$$3\lambda^2 + 2a\lambda - K^2 < 0. \tag{3.28}$$

Without loss of generality, we assume $K = 1$. Then (3.28) becomes

$$3\lambda^2 + 2a\lambda < 1. \tag{3.29}$$

To apply our theorem, we require the following

$$\frac{d}{dx}\left(\frac{\frac{x}{a+x}\big(1 - \frac{3x^2}{K^2} - \frac{2ax}{K^2}\big)}{-\gamma + \beta\frac{ax}{a+x}}\right) \le 0 \qquad \text{for } 0 \le x \le 1,$$

$$\Leftrightarrow \frac{d}{dx}\left(\frac{x(3x^2 + 2ax - 1)}{(\alpha\beta - \gamma)x - \gamma a}\right) \ge 0$$

$$\Leftrightarrow \frac{d}{dx}\left(\frac{x(3x^2 + 2ax - 1)}{x - \lambda}\right) \ge 0$$

$$\Leftrightarrow D(x) = 6x^3 + (2a - 9\lambda)x^2 - 4a\lambda x + \lambda \ge 0. \tag{3.30}$$

Note $D(0) = \lambda > 0$.

$$D'(x) = 18x^2 + 2(2a - 9\lambda)\alpha - 4a\lambda$$

$$= 2(x - \lambda)(9x + 2a)$$

Hence $D'(x) \geq 0$ for $x \geq \lambda$ and $D'(x) \leq 0$ for $x \geq 0$. Therefore $D(x) \geq D(\lambda)$ for $x \geq 0$. However, $D(\lambda) = \lambda(1 - 2a\lambda - 3\lambda^2) > 0$. This implies that for $\theta = 2$, $m = 1$ in system (3.27), if the unique positive equilibrium $(\bar{x}, \bar{y})$ is unstable, then there is a unique limit cycle surrounding it.

Example 3. We consider

$$\begin{aligned} \frac{dx}{dt} &= x(\frac{1}{4} + 2x - x^2 + x^3 - \frac{1}{4}x^4 - y) \\ \frac{dy}{dt} &= \gamma y(-1 + x) \end{aligned} \tag{3.31}$$

Let $g(x) = \frac{1}{4} + 2x - x^2 + x^3 - \frac{1}{4}x^4$, then its derivative is $g'(x) = 2 - 2x + 3x^2 - x^3 = 2 + (x - 1) - (x - 1)^3$. It can be shown that there is a K, $3 < K < 4$, such that $g(x)(x - K) < 0$ when $x \neq K$. Obviously, the unique interior equilibrium is E(1,2). We note $g'(1) = 2 > 0$, which means E(1.2) is unstable. Since $p(x) = x$, therefore (3.20) is equivalent to

$$\begin{aligned} 0 \geq \frac{d}{dx}\left(\frac{xg(x)}{-\gamma + q(x)}\right) &= \frac{d}{dx}\left(\frac{x(2 + (x - 1) - (x - 1)^3}{x - 1}\right) \\ &= \frac{1}{(x - 1)^2}(x(x - 1)^2(-3x + 4) - 2) \end{aligned} \tag{3.32}$$

Now let $L(x) = x(x - 1)^2(-3x + 4)$, then (3.32) is equivalent to $L(x) \leq 2$, $0 \leq x \leq K$.

We observe that when $0 \le x \le 1$, $x(1-x) \le \frac{1}{4}$, hence $L(x) \le \frac{1}{4}(1-x)(-3x+4) \le \frac{1}{4} \cdot 1 \cdot 4 = 1 < 2$; when $1 \le x \le \frac{4}{3}$, $L(x) \le \frac{4}{3} \cdot \frac{1}{9} = \frac{4}{27} < 2$; when $x > \frac{4}{3}$, $L(x) < 0 < 2$. Therefore for $x > 0$, $L(x) < 2$, i.e.

$$\frac{d}{dx}\left(\frac{xg'(x)}{-\gamma + q(x)}\right) < 0, \text{when } x \neq 1$$

proving the uniqueness of the limit cycle of system (3.31).

The careful reader may find that in the previous three examples, the condition (3.20) is satisfied automatically when the corresponding system has a unique unstable positive equilibrium. However, this is not always the case, as the following example will illustrate.

Example 4. We consider

$$\begin{aligned} \frac{dx}{dt} &= ax(b + \alpha(x-\gamma) - \beta(x-\gamma)^3 - y) \\ \frac{dy}{dt} &= cy(-\gamma + x) \end{aligned} \tag{3.33}$$

where a, b, c, α, β, γ are positive constants and $b > \frac{4\alpha}{3}\sqrt{\frac{\alpha}{3\beta}}$.

Denote $g(x) = a(b + \alpha(x-\gamma) - \beta(x-\gamma)^3)$, and assume: $p(x) = ax$, $q(x) = x$, $\xi(y) = y$, $\eta(y) = cy$. Denote $h(x) = xg(x)/p(x)$. Then

$$h(x) = b + \alpha(x-\gamma) - \beta(x-\gamma)^3 \tag{3.34}$$

and $h'(x) = \alpha - 3\beta(x-\gamma)^2$. It is clear that the unique positive equilibrium of system (3.33) is (γ, b), and $h'(\gamma) = \alpha > 0$, which implies (γ, b) is unstable by the criterion of Rosenzweig and MacArthur.

Since the roots for $h'(x) = 0$ are $x = \gamma \pm \sqrt{\frac{\alpha}{3\beta}}$, we see that the minimum value of $h(x)$ in $[0, \gamma]$ is $h_{\min} = b - \alpha\sqrt{\frac{\alpha}{3\beta}} - \frac{\alpha}{3}\sqrt{\frac{\alpha}{3\beta}} = b - \frac{4\alpha}{3}\sqrt{\frac{\alpha}{3\beta}} > 0$ which shows that $h(x)$ is a standard prey isocline.

We note

$$\frac{p(x)h'(x)}{-\gamma + q(x)} = a\left(\alpha + \frac{\alpha\gamma}{x-\gamma} - 3\beta x(x-\gamma)\right)$$

and hence

$$\begin{aligned}\frac{d}{dx}\left(\frac{p(x)h'(x)}{-\gamma + q(x)}\right) &= a\left(-\frac{\alpha\gamma}{(x-\gamma)^2} - 3\beta(2x-\gamma)\right) \\ &= \frac{-a}{(x-\gamma)^2}(\alpha\gamma + 3\beta(x-\gamma)^2(2x-\gamma)).\end{aligned} \tag{3.35}$$

Let $\phi(x) = \alpha\gamma + 3\beta(x-\gamma)^2(2x-\gamma)$. We see that $\phi(x) > 0$ when $2x - \gamma > 0$. The minimum of $\phi(x)$ in $[0, \gamma/2]$ is achieved at $x = 0$, and is $\alpha\gamma - 3\beta\gamma^3 = \gamma(\alpha - 3\beta\gamma^2)$. Therefore, when $\alpha \geq 3\beta\gamma^2$, then for all $x > 0$,

$$\frac{d}{dx}\left(\frac{p(x)h'(x)}{-\gamma + q(x)}\right) \leq 0, \tag{3.36}$$

i.e. if $\alpha \geq 3\beta\gamma^2$, then system (3.33) possesses a unique limit cycle in the positive cone.

It can be shown that all the previous four examples can be transformed into the system considered by Liou and Cheng (1986) as in section 3.2, after a suitable change of variables.

However, the following example cannot be transformed into any system for which uniqueness of limits cycles has been established in previous papers. This is because the prey isocline in the following example does not satisfy the condition

(2) as required in Liou and Cheng's (1986) result, which is essential for their analysis to be carried out.

Example 5. We consider

$$\begin{aligned} \frac{dx}{dt} &= x(g(x)-y),\ x(0)=x_0>0 \\ \frac{dy}{dt} &= y(-1+x),\ y(0)=y_0>0 \end{aligned} \tag{3.37}$$

where $g(x)$ is defined as follows:

$$g(x)=\begin{cases} 1 & 0\le x<\frac{1}{2} \\ 1+(x-\frac{1}{2})^2 & \frac{1}{2}\le x<1 \\ \frac{7}{4}-\frac{1}{2}(x-2)^2 & x\ge 1. \end{cases}$$

It is easy to see that $g(x)$ is continuously differentiable, and obviously does not satisfy the condition (2) in Liou and Cheng's (1988) result. We observe $E(1,\frac{5}{4})$ is the unique positive equilibrium of (3.37). Further, $g'(1)=1>0$. Hence $E(1,\frac{5}{4})$ is unstable. We note that

$$\frac{d}{dx}\left(\frac{xg'(x)}{x-1}\right)=\begin{cases} 0 & 0\le x<\frac{1}{2} \\ \frac{2x^2-4x+1}{(x-1)^2}<0 & 0\le x<1 \\ \frac{-(x-1)^2-1}{(x-1)^2}<0 & x\ge 1. \end{cases}$$

Hence, by Theorem 3.6, we conclude that there is a unique limit cycle of system (3.37) in the positive cone.

3.6 Discussion

By transforming a class of predator-prey models into a generalized Lienard system, we have obtained criteria for uniqueness of stable limit cycles when they exist. Although Cherkas and Zhilevich's result appeared in the early seventies, the relationship between Lienard system and Gause-type predator-prey system

was totally unknown until very recently (see Kuang and Freedman (1988)). However, the results on the generalized Lienard system by Zhang have only recently been published in the English language.

By examining the proof of Theorem 3.2 in the appendix, we can see our results can be generalized to some Kolmogorov-type predator-prey systems. However, strong conditions will be required to ensure that the method of Zhang is applicable to the more general system. These conditions may be very hard to satisfy and/or verify.

We note that for the first three examples illustrated in this chapter, the inequality (3.20) is automatically satisfied when the unique positive equilibrium is unstable. This makes the artificial condition (3.20) seem quite natural. However, this fails to be true in the case of example 4. In the next chapter, we will describe an example of a Gause-type predator-prey system with a unique unstable positive equilibrium and having at least three limit cycles surrounding it.

Appendix

Proof of Theorem 3.2. We prove this result for $f(0) < 0$. The proof in the case $f(0) > 0$ follows analogously. The system (3.2) has a unique equilibrium $(0,0)$, which is unstable. We first suppose that there are two limit cycles, L_1 and L_2, where L_1 is the closest to the origin and L_2 is any cycle surrounding L_1. Let

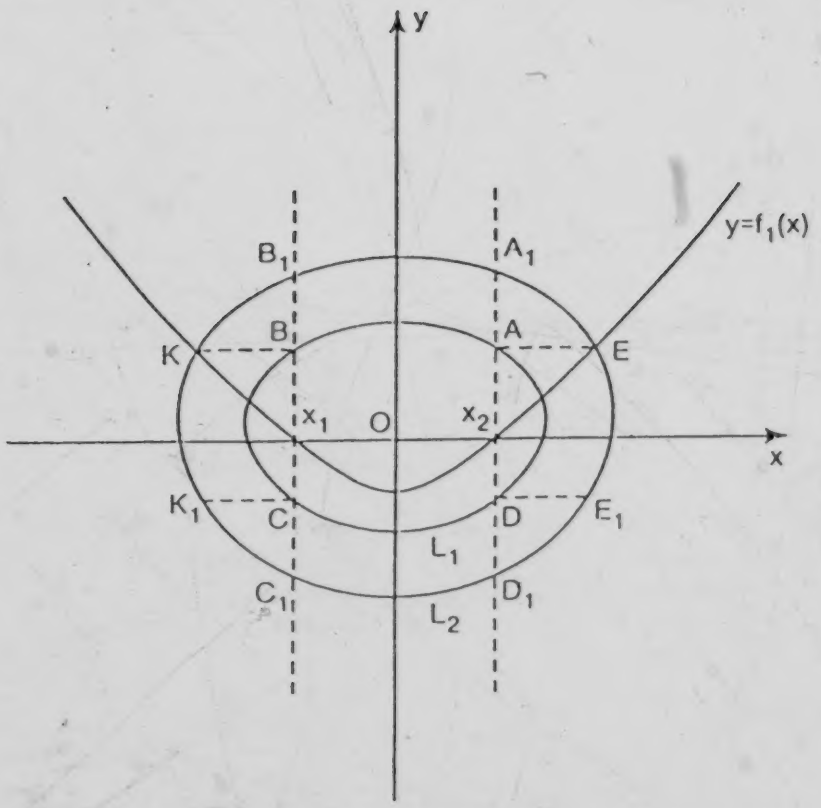

Figure 3.1. The system (3.2) with a unique equilibrium at (0,0) and surrounded by two limit cycles L_1 , L_2 .

$x(t)$, $y(t)$ be solutions of (3.2). Then

$$\begin{aligned} &\oint_{L_i} h(x)dt = 0, \qquad \oint_{L_i} h(x)\varphi(y)dt = 0 \\ &\oint_{L_i} h(x)(\varphi(y) + F(x))dt = 0; \qquad i = 1,2, \end{aligned} \tag{A.1}$$

since along L_i, $x(t)$ and $y(t)$ are periodic solutions. Thus from (3.3) we can see that the integral of the divergence, $-f(x)$, of (3.2) satisfies the equality

$$h_i \overset{\text{def}}{=} -\oint_{L_i} f(x)dt = -\oint_{L_i} f_1(x)dt, \qquad i = 1,2. \tag{A.2}$$

We shall prove that $h_2 < h_1$. To this end, we consider Fig. 3.1. By Green's formula, we have

$$\begin{aligned} \int_{E_1E} f_1(x)dt - \int_{DA} f_1(x)dt &= \int_{E_1EADE_1} \frac{f_1(x)}{h(x)}\,dy \\ &= \int\int_{S_1} \frac{d}{dx}\Big(\frac{f_1}{h}\Big)dxdy \geq 0 \\ \int_{A_1B_1} f_1(x)dt - \int_{AB} f_1(x)dt &= -\int_{A_1B_1BAA_1} \frac{f_1(x)dx}{\varphi(y) + F(x)} \\ &= -\int\int_{S_2} \frac{f_1(x)\varphi'(y)}{[\varphi(y) + F(x)]^2}\,dxdy \geq 0 \end{aligned}$$

where S_1 and S_2 are the two regions bounded by the above two closed paths respectively. Similarly, we have

$$\begin{aligned} \int_{KK_1} f_1(x)dt &\geq \int_{BC} f_1(x)dt \\ \int_{C_1D_1} f_1(x)dt &\geq \int_{CD} f_1(x)dt. \end{aligned}$$

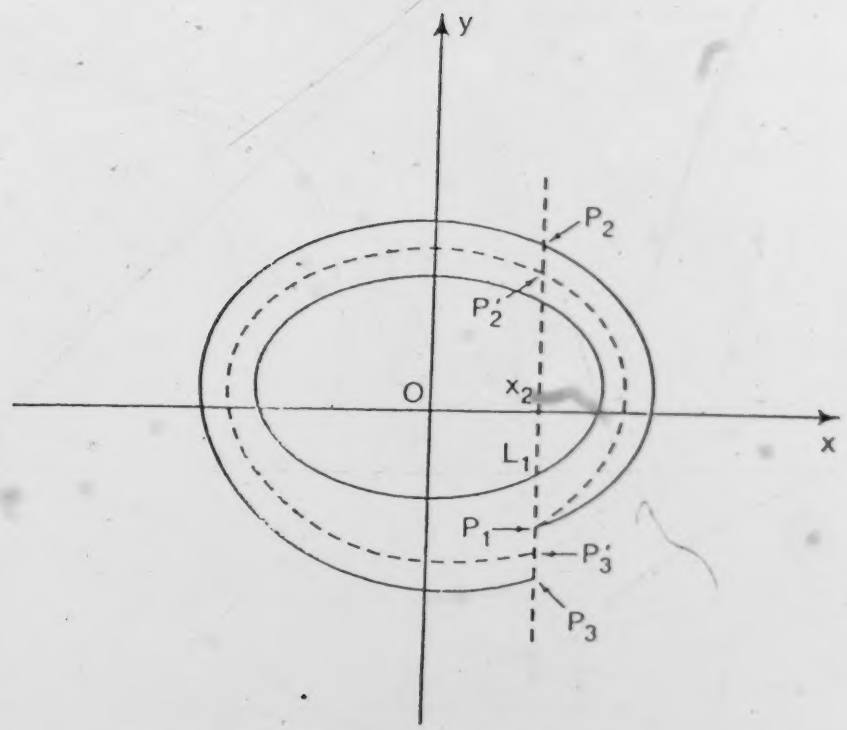

Figure 3.2. The system (A.3) and (3.2). Solid line represents orbits in (3.2), dashed line represents orbits in (A.3).

Moreover, we have the obvious inequalities

$$\int_{B_1K} f_1(x)dt > 0; \qquad \int_{EA_1} f_1(x)dt > 0$$
$$\int_{K_1C_1} f_1(x)dt > 0; \qquad \int_{D_1E_1} f_1(x)dt > 0.$$

Hence $h_2 < h_1$.

However, we already know that $(0,0)$ is unstable. Hence L_1 is internally stable. By Poincaré's criterion of stability, we know that $h_1 \leq 0$, which implies $h_2 < 0$. If we can prove L_1 is not a semistable cycle, but a stable one, then we know L_2 cannot exist. Since if L_1 is externally stable, L_2 must be internally unstable, giving $h_2 \geq 0$, which contradicts the fact that $h_2 < 0$.

Now suppose L_1 is a semistable cycle. Suppose $\beta \geq 0$ (the argument is similar when $\beta < 0$). We construct a system of equations depending on the parameter γ, where $\gamma > 0$:

$$\begin{aligned} \frac{dx}{dt} &= -\varphi(y) - \overline{F}(x) \\ \frac{dy}{dt} &= h(x), \end{aligned} \tag{A.3}$$

where

$$\overline{F}(x) = \begin{cases} F(x) & \text{when } x \leq x_2 \\ F(x) + \int_{x_2}^{x} \gamma(\varsigma - x_2)h(\varsigma)d\varsigma & \text{when } x > x_2. \end{cases} \tag{A.4}$$

Note that system (A.3) and system (3.2) are identical in the half-plane $x \leq x_2$, and the new system (A.3) forms a family of rotated vector fields with respect to γ in the half-plane $x > x_2$, and hence forms a family of generalized rotated vector fields in the whole plane.

The function $\overline{F}(x)$ satisfies all conditions of the theorem. A comparison of the direction fields for (3.2) and (A.3) shows that since L_1 is supposed to be semistable, system (3.2) has an orbit arc of the form $P_1P_2P_3$ (see Fig. 3.2). For sufficiently small γ system (A.3) has an orbit arc $P_1P_2'P_3'$. Hence in the region bounded by the curves $P_1P_2'P_3'P_1$ and L_1, the system (A.3) has a limit cycle $\overline{L}_2$ with $\overline{h}_2 \geq 0$, and inside L_1 a cycle $\overline{L}_1$ with $\overline{h}_1 \leq 0$, i.e., $\overline{L}_2$ surrounds $\overline{L}_1$. But $\overline{h}_1 \leq \overline{h}_2$. This is a contradiction. Hence L_1 is stable, proving the theorem.

CHAPTER IV

NONUNIQUENESS OF LIMIT CYCLES IN GAUSE-TYPE PREDATOR-PREY SYSTEMS

4.1 Introduction

As we have pointed out earlier, Gause-type predator-prey systems have been extensively investigated in the last few decades. However, most of the work done concerns the existence and local stability of equilibria and periodic solutions, or Hopf bifurcation phenomena. Although there are several papers which address the topic of global stability of the unique interior equilibrium for some very specific Gause-type predator-prey models, almost no work related to uniqueness or nonuniquenss of limit cycles in general predator-prey systems has been done.

At the time Hsu (1978) published his result showing that local asymptotic stability of an interior equilibrium of certain Gause-type predator-prey systems, together with the existence of a concave down prey isocline, implied that this equilibrium was globally asymptotic stable, H.I. Freedman (Personal communciation, also see Kuang and Freedman, 1988) conjectured that if the equilibrium were unstable instead of stable, implying the existence of a limit cycle, then this limit cycle is unique. This conjecture seems to be reinforced by the result of Cheng (1981) and those examples in the pervious chapter of this thesis (also see Kuang and Freedman (1988)). However, it turns out that the conjecture is not always true. It is the main purpose of this chapter to construct a counterexample of this conjecture.

In the following section, we prove a general theorem concerning the nonuniqueness of limit cycles of Gause-type predator-prey systems. In section 4.3, we construct a counterexample to H.I. Freedman's conjecture. The final section contains a brief discussion.

4.2 A nonuniqueness theorem

As in the previous chapter, we consider the following Gause-type predator-prey system

$$\begin{aligned} \dot{x} &= xg(x) - \xi(y)p(x), \quad x(0) = x_0 \geq 0 \\ \dot{y} &= \eta(y)(-\gamma + q(x)), \quad y(0) = y_0 \geq 0. \end{aligned} \tag{4.1}$$

We assume throughout this chapter that (4.1) satisfies (H1) to (H8) inclusively.

In this section, we establish criteria for there to be at least three limit cycles for system (4.1). First we require some lemmas.

LEMMA 4.1. *Assuming (H2) to (H7) hold for the following system*

$$\begin{aligned} \dot{x} &= p(x)\big(\beta - \xi(y)\big), \quad x(0) = x_0 > 0 \\ \dot{y} &= \eta(y)\big(-\gamma + q(x)\big), \quad y(0) = y_0 > 0, \end{aligned} \tag{*}$$

where $\beta > 0$ is a constant, then every trajectory of (*) is a closed orbit (except the equilibrium $E^*(x^*, y^*)$).

Proof. We note the following:

$$\frac{dy}{dx} = \frac{\eta(y)\big(-\gamma + q(x)\big)}{p(x)\big(\beta - \xi(y)\big)},$$

or

$$\frac{\beta - \xi(y)}{\eta(y)}\, dy = \frac{-\gamma + q(x)}{p(x)}\, dx.$$

Hence

$$\int_{y_0}^{y} \frac{\beta - \xi(y)}{\eta(y)}\, dy = \int_{x_0}^{x} \frac{-\gamma + q(x)}{p(x)}\, dx$$

Consider the trajectory $(x(t), y(t))$, with $x(0) = x_0$, $y(0) = y_0$, and $(x_0, y_0) \neq (x^*, y^*)$. Then there is a sequence $t_1 < t_2 < \cdots < t_{2n-1} < t_{2n} \ldots$, such that $x(t_n) = x^*$, $0 < y(t_{2n-1}) < y^*$, $y(t_{2n}) > y^*$. If $(x(t), y(t))$ is not a closed orbit, then $y(t_3) \neq y(t_1)$. Assume $y(t_3) > y(t_1)$, then

$$\int_{y_0}^{y(t_3)} \frac{\beta - \xi(y)}{\eta(y)}\, dy = \int_{y_0}^{y(t_1)} \frac{\beta - \xi(y)}{\eta(y)}\, dy + \int_{y(t_1)}^{y(t_3)} \frac{\beta - \xi(y)}{\eta(y)}\, dy$$

Since $\beta - \xi(y) > 0$, when $y < y^*$, therefore

$$\int_{x_0}^{x^*} \frac{-\gamma + q(x)}{p(x)}\, dx = \int_{y_0}^{y(t_3)} \frac{\beta - \xi(y)}{\eta(y)}\, dy < \int_{y_0}^{y(t_1)} \frac{\beta - \xi(y)}{\eta(y)}\, dy = \int_{x_0}^{x^*} \frac{\gamma + q(x)}{p(x)}\, dx,$$

a contradiction. The case that $y(t_3) < y(t_1)$ can be analysed in the same manner. This completes the proof.

LEMMA 4.2. *Consider the following system*

$$\begin{aligned} \dot{x} &= p(x)(h_i(x) - \xi(y)) \\ \dot{y} &= \eta(y)(-\gamma + q(x)) \end{aligned} \qquad (4.2_i)$$

$$x(0) = x_0 > 0\,,\ y(0) = y_0 > 0\,,\ i = 1, 2$$

Let $h_1(x^*) = h_2(x^*)$, *where* $x^* = q^{-1}(\gamma)$, *and* $y^* = \xi^{-1}(h_1(x^*))$. *Suppose*

$$\begin{aligned} &h_1(x) \geq h_2(x), \text{ when } x^* \leq x \leq K\,, \\ &h_1(x) \leq h_2(x) \text{ when } 0 \leq x \leq x^* \end{aligned} \qquad (4.3)$$

with strict inequality holding for some values of x *on* $0 \le x \le x^*$ *and* $x^* \le x \le K$. *Denote* $P_0 = (x^*, y_0), y_0 < y^*$, $P_{i1} = (x^*, y_{i1}(y_0))$, *where* $y_{i1}(y_0) > y^*$ *and* $Q_i = (x_{is}(y_0), y^*)$, *where* $0 < x_{is}(y_0) < x^*$, $P_{i2} = (x^*, y_{i2}(y_0))$, *and* $0 < y_{i2}(y_0) < y^*$. $P_{i1}, Q_i, P_{i2} \in L_i((x^*, y_0)), i = 1, 2$, *where* $L_i((x^*, y_0))$ *is the orbit of* (4.2_i) *starting at* P_0. *We assume* P_{i1}, Q_i, P_{i2} *are the first points of* $L_i((x^*, y_0))$ *(according to the time spent) having the above described properties. Then we have*

(i) $y_{11}(y_0) > y_{21}(y_0)$

(ii) $y_{12}(y_0) < y_{22}(y_0)$

(iii) $x_{1s}(y_0) < x_{2s}(y_0)$

(iv) $y_{i2}(y_0) < h_i(x_{is}(y_0))$, *if* $h_i'(x) \ge 0$, *when* $0 \le x \le x^*$, $i = 1, 2$.

Proof. Let

$$\vec{v}_1 = (p(x)(h_1(x) - \xi(x)), \quad \eta(y)(-\gamma + q(x)), 0)$$

$$\vec{v}_2 = (p(x)(h_2(x) - \xi(x)), \quad \eta(y)(-\gamma + q(x)), 0).$$

Then $\vec{v}_1 \times \vec{v}_2 = (0, 0, p(x)\eta(y)(-\gamma + q(x))(h_1(x) - h_2(x)))$ We note that

$$p(x)\eta(y)(-\gamma + q(x))(h_1(x) - h_2(x)) \ge 0.$$

Hence the flow of (4.2_1) is always directed outwards with respect to the flow of (4.2_2). Therefore (i), (ii) and (iii) are verified.

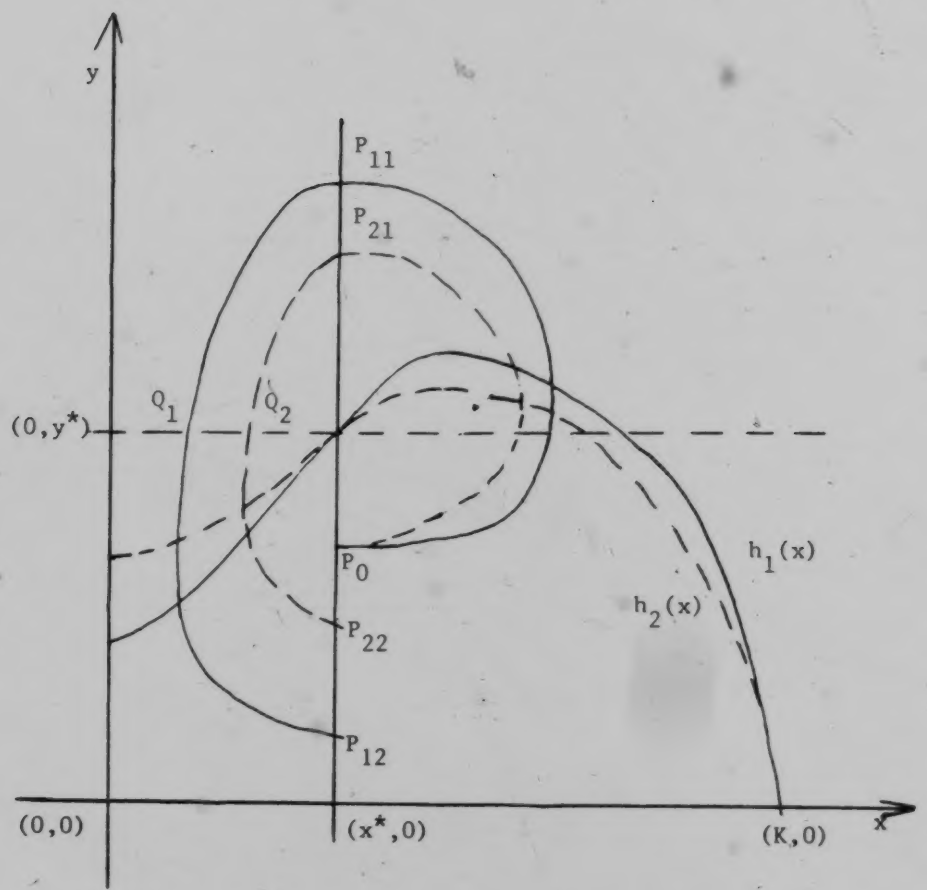

Figure 4.1. The relationship between prey isoclines and orbits of system (4.2i).

Suppose $h_1'(x) \geq 0$, $0 \leq x \leq x^*$, $i = 1, 2$. We first observe that when $0 \leq x \leq x^*$, $\frac{dy}{dx} \leq 0$. Assume $L_i((x^*, y_0))$ intersects with $(x, h_i(x))$ at $(x_i(y_0), h_i(x_i(y_0)))$. Then we have

$$x_i(y_0) \leq x_{i2}(y_0).$$

Hence $y_{i2}(y_0) \leq h_i(x_i(y_0)) \leq h_i(x_{i2}(y_0))$. Therefore (iv) holds (see Fig. 4.1).

Now, we are in the position to state and prove our main theorem.

THEOREM 4.3. *Consider system (4.1) and let (H1)-(H8) hold. Further assume*

(i) $(xg(x)/p(x))' \geq 0$, *when* $0 \leq x \leq x^*$.

(ii) $xg(x)/p(x) \geq a_1 > 0$, *when* $x^* \leq x \leq x_1$.

Denote $a_2 = \xi(y^*)$. *Let* $\Gamma_i(x_0, y_0) = (x_i(t, x_0, y_0), y_i(t, x_0, y_0))$ *represent the orbit of*

$$\begin{aligned} \dot{x} &= p(x)(a_i - \xi(y)) \\ \dot{y} &= \eta(y)(-\gamma + q(x)), \end{aligned} \tag{4.4$_i$}$$

$x(0) = x_0 > 0$, $y(0) = y_0 > 0$, $i = 1, 2$. *Let*

$$\begin{aligned} y_M(y_0) &= \max_{t \in [0,\infty)} y_1(t, x^*, y_0) \\ \bar{x}(y_0) &= \min_{t \in [0,\infty)} x_2(t, x^*, y_M(y_0)), \end{aligned}$$

(iii) Assume there is a stable limit cycle surrounding $E^*(x^*, y^*)$, *which is contained in the circle*

$$(x - x^*)^2 + (y - y^*)^2 \leq r^2, \quad r > 0.$$

(iv) There is a $\bar{y}$, *such that* $0 < \bar{y} < y^* - r$ *and* $\Gamma_1(x^*, \bar{y}_0) \subset \{(x, y) | 0 < x < x_1, y > 0\}$, *and* $\frac{\bar{x}(\bar{y})g(\bar{x}(\bar{y}))}{p(\bar{x}(\bar{y}))} \leq \bar{y}$.

Then, system (4.1) has at least three limit cycles.

Proof. Define $h_1(x) = xg(x)/p(x)$, $h_2(x) = \begin{cases} h_1(x) & x_1 < x \le K \\ a_1 & x^* < x \le x_1 \\ a_2 & 0 \le x \le x^* \end{cases}$.

In what follows, $y_{ij}(y_0)$, $i = 1, 2$; $j = 1, 2$ and $x_{is}(y_0)$ $i = 1, 2$, have the same meaning as in Lemma 4.2. Although $h_2(x)$ may not be continuous, it is easy to see that Lemma 4.2 is still true in this case. Denote $\alpha(y_0) = y_0 - y_{12}(y_0)$.

Since (x^*, y^*) is unstable, then $\alpha(y_0) \neq 0$ when y_0 is very close to y^*. By (iii) there is a y_1 such that $y^* - r \le y_1 < y^*$, and $\alpha(y_1) = 0$. Also there is a $\delta_1 > 0$, such that when $y_1 - \delta_1 < y_0 < y_1$, then $\alpha(y_0) < 0$.

By virtue of Lemma 4.2;

$$y_{12}(y_0) \le \frac{\bar{x}(y_0)g(\bar{x}(y_0))}{p(\bar{x}(y_0))}.$$

Hence by (iv), there is $\bar{y}$, $0 < \bar{y} < y^* - r$, such that

$$y_{12}(\bar{y}) < \bar{y}, \text{ i.e. } \alpha(\bar{y}) > 0.$$

Moreover, by the dynamics of system (4.1), we know there exists a δ_2, $\delta_2 > 0$, such that when $0 < y_0 < \delta_2$, then $\alpha(y_0) < 0$. Therefore, by the continuity of $\alpha(y_0)$ (since $y_{12}(y_0)$ is continuous), there exists $y_2, y_3, \bar{y} < y_2 < y_1 - \delta_1$, $0 < y_3 < \bar{y}$, such that

$$\alpha(y_2) = \alpha(y_3) = 0.$$

It is obvious, that each solution of $\alpha(y_0) = 0$ corresponding to a limit cycle (periodic solution) of the system (4.1). This completes the proof.

4.3 A counterexample to Freedman's conjecture

In this section we assume $\xi(y) = \eta(y) = y$ in (4.1). In Chapter III the following result is obtained

THEOREM. *(Y. Kuang and H.I. Freedman (1988)) Suppose in system (4.1)*

$$\frac{d}{dx}\left(\frac{xg'(x) + g(x) - xg(x)\frac{p'(x)}{p(x)}}{-\gamma + q(x)}\right) \leq 0 \tag{4.5}$$

and $0 \leq x < x^*$ and $x^* < x \leq K$. Then system (4.1) has exactly one limit cycle which is globally asymptotically stable with respect to the set $\{(x,y) | x > 0, y > 0\} \setminus \{E^*\}$, where $E^* = (x^*, y^*)$ is the unique unstable positive equilibrium.

It is clear that assumptions (H1) to (H8) are not sufficient to guarantee the uniqueness of limit cycles of (4.1). Inequality (4.5) is sufficient but not necessary. When $q(x) = cp(x) = \delta x$, and $g(x) = \alpha(x + \theta)(K - x)$, where α, θ, K, δ, $c > 0$ are constants, we know that (4.1) has a unique limit cycle. In this case, $\frac{xg(x)}{p(x)} = \frac{c}{\delta}\alpha(x+\theta)(K-x)$ is a strictly concave function. Supported by some other related facts both mathematically and ecologically, H.I. Freedman posed the following conjecture [Kuang and Freedman (1988)].

CONJECTURE. *(H.I. Freedman) Assume (H1) to (H8) hold for (4.1). Furthermore, if the prey isocline $y = xg(x)/p(x)$ is strictly concave down, then (4.1) has a unique limit cycle.*

In what follows, we present a counterexample to this conjecture showing that the conjecture is not always true. The technique utilized here can be ex-

tended to construct examples that have $2n+1$ limit cycles, while all the assumptions of the conjecture continue to be satisfied, and n is any prescribed positive integer.

To construct the counterexample, we need some lemmas.

LEMMA 4.4. *Consider*

$$\begin{aligned} \dot{x} &= x(1-y) \\ \dot{y} &= \delta y(-1+x) \end{aligned} \tag{4.6}$$

$x_0 = x(0) = 1, 0 < y_0 = y(0) < 1, \delta > 0$ *is a constant. Then the solution orbit* $L((1,y_0))$ *of (4.6) initiating at* $(1,y_0)$ *satisfies*

$$\delta(x-1) - \delta \ell n\ x + y - 1 - \ell n\ y = y_0 - 1 - \ell n\ y_0\,. \tag{4.7}$$

Now, suppose $(x_s(y_0),1) \in L((1,y_0))$, *where* $x_s(y_0) < 1$. *Then* $\delta(x_s(y_0) - 1 - \ell n\ x_s(y_0)) = y_0 - 1 - \ell n\ y_0$. $f(x) = x - 1 - \ell n\ x$ *is a convex, positive definite function achieving its minimum, 0, at* $x = 1$. *Moreover, if* $x_1 - 1 - \ell n\ x_1 = x_2 - 1 - \ell n\ x_2$, *where* $0 < x_1 < 1$, *and* $x_2 > 1$, *then* $x_2 - 1 > 1 - x_1$. *Further, we have*

(i) when $\delta = 1$, $x_s(y_0) = y_0$;

(ii) when $\delta > 1$, $x_s(y_0) > y_0$, *and when* $\delta \to \infty$, $x_s(y_0) \to 1$, *i.e.,* $1 - x_s(y_0) \to 0$;

(iii) when $\delta < 1$, $x_s(y_0) < y_0$, *and when* $\delta \to 0$, $x_s(y_0) \to 0$, *i.e.,* $1 - x_s(y_0) \to 1$.

LEMMA 4.5. *Consider the following system with a parameter* μ.

$$\begin{aligned} \dot{x} &= x\left(1+\frac{1}{4}\mu^2-\frac{1}{4}(x-1-\mu)^2-y\right) \\ \dot{y} &= \delta y(-1+x) \end{aligned} \tag{4.8_μ}$$

Then, there is a supercritical Hopf bifurcation when $\mu = 0$, *and the limit cycle is unique.*

Proof We note that $(1,1)$ is the unique positive equilibrium for (4.8_μ). Its variational matrix at $(1,1)$ is

$$\begin{bmatrix} \frac{1}{2}\mu & -1 \\ \delta & 0 \end{bmatrix}.$$

Hence its eigenvalues are

$$\lambda_{1,2} = \frac{1}{4}\left(\mu \pm \sqrt{\mu^2-16\delta}\right)$$

$$\lambda_{1,2}(0) = \pm\sqrt{\delta}\,i \text{ and } \frac{d(\text{Re }\lambda(\mu))}{d\mu}\Big|_{\mu=0} = \frac{1}{4} > 0.$$

Therefore, (4.8_μ) exhibits a supercritical Hopf bifurcation when $\mu = 0$, by the Hopf bifurcation theorem [Marsden et al (1977)]. The uniqueness of the limit cycle follows from the results of [Cheng (1981)] or the first example in Chapter III.

COUNTEREXAMPLE. Let $y_0 = \frac{9}{10}$. Choose δ_0 so small, that when $\delta \le \delta_0$, $1 - x_s(y_0) \ge 4(1-y_0)$ for (4.6), i.e., $1 - x_s(y_0) \ge \frac{4}{10}$, or $x_s(y_0) \le \frac{6}{10}$. Let $(1, y_1(y_0))$, $(x_b(y_0), 1)$ lie on $L((1,y_0))$ for (4.6) when $\delta = \delta_0$, where $y_1(y_0) > 1$,

and $x_b(y_0) > 1$. By (4.7), we see that $y_1(y_0) > 1 + \frac{1}{10}$, and $x_b(y_0) > 1 + \frac{4}{10}$. We assume further, that when $\delta \leq \delta_0$ and $|y_1 - y_0| < \frac{1}{10^2}$. Then

$$\frac{1 - x_s(y_0)}{1 - y_0} \geq 4. \tag{4.9}$$

Now, we consider the system

$$\begin{aligned} \dot{x} &= x(g(x) - y) \\ \dot{y} &= \delta_0 y(-1 + x) \end{aligned} \tag{4.10}$$

where $g(1) = 1$. There exists ε, $0 < \varepsilon < 1$, such that if

$$|g(x) - 1| < \varepsilon \text{ for } 1 \leq x \leq x_b(y_0) + 1, \tag{4.11}$$

then

$$\begin{aligned} |y_{1g}(y_0) - y_1(y_0)| &< \frac{1}{10^3} \\ \text{and } |x_{jg}(y_0) - x_j(y_0)| &< \frac{1}{10^3} \end{aligned} \tag{4.12}$$

where $y_{1g}(y_0)$ and $x_{jg}(y_0)$, $j = b, s$, have similar meaning as $y_1(y_0)$, $x_j(y_0)$, $j = b, s$. Let $L_g((1, y_0))$ denote the orbit of (4.10) starting at $(1, y_0)$. Then $(1, y_{1g}(y_0)) \in L_g((1, y_0))$, where $y_{1g}(y_0) > 1$, and $(1, y_{1g}(y_0))$ is the first point of intersection of $L_g((1, y_0))$ with the line $x = 1$, $x_{bg}(y_0) > 1$, $x_{sg}(y_0) < 1$, $(x_j g(y_0), 1)$, $j = s, b$, is the first intersection point of $L_g((1, y_0))$ with $y = 1$ such that $x_{bg}(y_0) > 1$, $x_{sg}(y_0) < 1$.

By virtue of Lemma 4.5 we can choose μ_0 so small, that the unique limit cycle of (4.8_μ) has size of r_0, which is less than $(10^2(x_b(y_0) + 1))^{-1}$, and when

$$\begin{aligned} 1 - r_0 \leq x \leq 1 + r_0 \\ |\frac{1}{4}\mu_0^2 - \frac{1}{4}(x - 1 - \mu_0)^2| < \min\{\frac{\varepsilon}{4}\ ,\ \frac{1}{10^2(x_b(y_0) + 1)}\} \end{aligned} \tag{4.13}$$

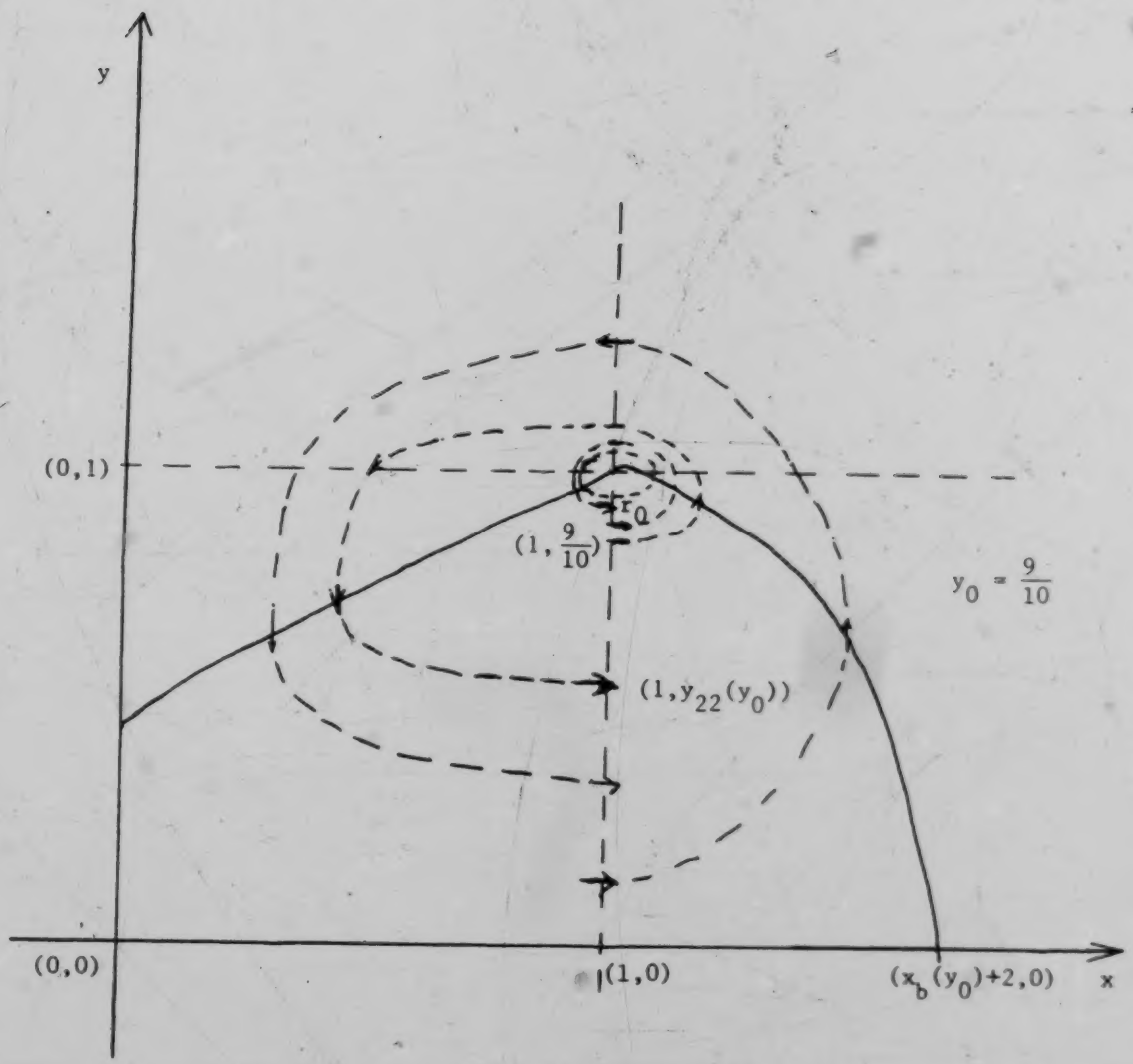

Figure 4.2 An illustration of the counterexample.

Here the size r_0 means that the limit cycle of (4.8_μ) will be contained in the region

$$\Delta = \{(x,y) | \, 1 - r_0 \leq x \leq 1 + r_0, \, 1 - r_0 \leq y \leq 1 + r_0\}.$$

Moreover, we can require

$$r_0 + \mu_0 < \frac{\varepsilon_1}{2(x_b(y_0) + 1)}.$$

We define $g_{1\mu_0}(x)$ as

$$g_{1\mu_0}(x) = \begin{cases} 1 + \frac{1}{4}\mu_0^2 - \frac{1}{4}(x - 1 - \mu_0)^2 & 1 - r_0 \leq x < 1 + r_0 \\ \frac{1}{2}(r_0 + \mu_0)(x + r_0 - 1) + 1 - \frac{1}{4}r_0^2 - \frac{1}{2}r_0\mu_0 & 0 \leq x \leq 1 - r_0 \\ \frac{1}{2}(\mu_0 - r_0)(x - 1 - r_0) + 1 - \frac{1}{4}r_0^2 + \frac{1}{2}r_0\mu_0 & 1 + r_0 \leq x \leq x_b(y_0) + 1 \\ h(x) & x_b(y_0) + 1 \leq x \leq x_b(y_0) + 2 \end{cases}$$

where $h(x)$ will be a strict concave down function such that

$$h(x_b(y_0) + 1) = \frac{1}{2}(\mu_0 - r_0)(x_b(y_0) - r_0) + 1 - \frac{1}{4}r_0^2 + \frac{1}{2}r_0\mu_0$$

and $h(x_b(y_0) + 2) = 0$.

We see that $g_{1\mu_0}(x)$ is continuous and concave (but not strictly concave). Moreover,

$$|g_{1\mu_0}(x) - 1| < \frac{\varepsilon}{2} \text{ when } 0 \leq x \leq x_b(y_0) + 1.$$

Therefore, (4.12) holds for $g_{1\mu_0}$.

We retain that part of $g_{1\mu_0}(x)$ when $1 - r_0 \leq x \leq 1 + r_0$, and substitute the part of $g_{1\mu_0}(x)$ when $x \geq 1 + r_0$ by a strictly concave, continuous function $\phi(x)$, such that

$$\phi(1 + r_0) = g_{1\mu_0}(1 + r_0); \; \phi(x_b(y_0) + 2) = 0,$$

$$\text{and } |\phi(x) - g_{1\mu_0}(x)| < \frac{\varepsilon_1}{4} \text{ when } 1 + r_0 \leq \alpha \leq x_b(y_0) + 2.$$

Moreover, we replace the part of $g_{1\mu_0}(x)$ when $0 \le x \le 1 - r_0$ by $\Phi(x)$ which is strictly concave and continuous and

$$\Phi(1-r_0) = g_{1\mu_0}(1-r_0),\ \Phi'(x) > 0,\ |\Phi(x) - \ell(x)| < \frac{1}{10^2},\ \text{when } 0 \le x \le 1-r_0,$$

where $\ell(x) = \frac{1}{2} + \frac{1}{2}x$.

Denote the new function as $g_{2\mu_0}(x)$. By virtue of Lemma 4.2 and (4.9) we have

$$\begin{aligned} y_{22}(y_0) < g_{2\mu_0}(x_{2s}(y_0)) &< \frac{1}{2} + \frac{1}{2}x_{2s}(y_0) + \frac{1}{10^2} \\ &< \frac{1}{2} + \frac{1}{2}x_s(y_0) + \frac{2}{10^2} < \frac{1}{2} + \frac{3}{10} + \frac{2}{10^2} = \frac{8}{10} + \frac{2}{10^2} < \frac{9}{10} = y_0 \end{aligned}$$

where $y_{22}(y_0)$, $x_{2s}(y_0)$ is defined as in Lemma 4.2, where h_2 is replaced by $g_{2\mu_0}$.

We note that when $y_0 \to 0$, $y_{22}(y_0) > y_0$. Hence there is at least one other limit cycle which will envelope the region bounded by the part of the orbit of (4.10) (where $g = g_{2\mu_0}$) starting at $(1, \frac{9}{10})$, and ending at $(1, y_{22}(\frac{9}{10}))$ and the line $\{(x,y) | x = 1,\ y_{22}(\frac{9}{10}) \le y < \frac{9}{10}\}$. By Theorem 4.3 we know (4.10) has at least three limit cycles (see Fig. 4.2).

4.4 Discussion

In section 4.3, if we choose $\phi(x)$ and $\Phi(x)$ carefully, we can construct examples having more than n limit cycles, where n is any prescribed positive integer. Theorem 4.3 can be replaced by a similar theorem generated in a similar manner describing the above statement.

If we do not impose the concavity on $xg(x)/p(x)$ for system (4.1), then it is trivial to construct an example having at least two limit cycles. This is quite obvious from the procedure we presented here.

In the case (H8) fails to be true, the slightly modified version of a Lotka-Volterra system will give us an example having infinitely many periodic orbits (not limit cycles). However, in this situation, the strict concavity of $xg(x)/p(x)$ cannot be maintained. An example of a Kolmogorov system which has infinitely many periodic solutions (and two limit cycles) is given by Albrecht et al (1973).

By employing the Hopf bifurcation method, G. Wolkowicz (1987) pointed out that in the case there is a stable positive equilibrium, even the strict concavity together with symmetry of the prey isocline will still not be enough to guarantee the uniqueness of a limit cycle. In the case the interior equilibrium is unstable, Conway and Smoller (1986) claimed the uniqueness result for the special case of $p(x) = q(x) = x$, $\xi(y) = \eta(y) = y$. Unfortunately their proof is incorrect. However, the question of whether or not their claim is true (also for the general case) remains open.

Obviously the method and results of this chapter can be applied to the Gause-type predator-prey systems with group defence analysed by Freedman and Wolkowicz (1986) as well as the "asocial" predator-prey systems discussed by Conway and Smoller (1986).

CHAPTER V

LOCATION AND PERIOD OF LIMIT CYCLES IN GAUSE-TYPE PREDATOR-PREY SYSTEMS

5.1 Introduction

In this chapter, an attempt is made to estimate the location and period of the limit cycles of Gause-type predator-prey systems in the case that the positive equilibrium is unstable.

The question of determining the location and period of limit cycles also arose in papers dealing with the variational models of Gause-type predator-prey systems. Examples are the Lotka-Volterra systems (Hsu, 1978), in the so called "asocial" predator-prey system (Conway and Smoller (1986)), or the Gause-type predator-prey system with group defense as discussed recently by Freedman and Wolkowicz (1986). We point out here that the technique which will be developed in this chapter can be generalized so as to be applicable to all of the above mentioned systems.

The following section is devoted to a discussion of the location of limit cycles of Gause-type predator-prey systems, where an annular region which contains all the limit cycles is obtained. In section 3, we present an upper bound for the period of the limit cycles of the system. Both the annular region and the upper bound of the period are explicitly computable. We finish this chapter by a discussion, where some improvements of our previous uniqueness results will be mentioned.

5.2 Location of limit cycles

We still consider the Gause-type predator-prey system

$$\begin{aligned} \dot{x} &= xg(x) - \xi(y)p(x), \quad x(0) = x_0 \geq 0 \\ \dot{y} &= \eta(y)(-\gamma + q(x)), \quad y(0) = y_0 \geq 0 \end{aligned} \tag{5.1}$$

and again, we assume throughout this chapter that (5.1) satisfies (H1) to (H8) inclusively.

In this section, we first attempt to find a positively invariant set of (5.1) in the positive cone, then employ a comparison method to locate an annular region which contains all the limit cycles of system (5.1). Before stating and proving our theorem, we require some lemmas.

LEMMA 5.1. *Let $k > 0$ be a constant such that when $x \geq x^*$,*

$$k\xi(k(K-x))p(x) \geq kxg(x) + \eta(k(K-x))(-\gamma + q(x)). \tag{5.2}$$

Then the following set, I, is positively invariant for system (5.1), where $I = I_1 \cup I_2$ and where

$$I_1 = \{(x,y) \mid 0 \leq x \leq x^*, \quad 0 \leq y \leq k(K-x^*)\}$$

$$I_2 = \{(x,y) \mid x^* \leq x \leq K, \quad 0 \leq y \leq k(K-x)\}.$$

Proof. We first imbed the $x-y$ plane in R^3 space, denoting $\vec{u} = (\dot{x}, \dot{y}, 0)$ and $\vec{n} = (-1, s, 0)$ as the tangent vector (in R^3) of the positive boundary (interior to the positive cone of $x-y$ plane) of I. Then $\vec{n} \times \vec{u} = (0,\ 0,\ -(\dot{y} + s\dot{x}))$. Hence, proving the lemma is equivalent to proving that

$$\dot{y} + s\dot{x} \leq 0 \quad \text{when } 0 \leq x \leq K. \tag{5.3}$$

(i) When $0 \le x \le x^*$; $s = 0$, (5.3) is equivalent to $\dot{y} \le 0$, i.e., $\eta(y)(-\gamma + q(x)) \le 0$ which is obvious.

(ii) $x^* \le x \le K$. On the boundary $y = k(K - x)$, which in this case means $s = k$. Hence $\dot{y} + s\dot{x} \le 0$ is equivalent to

$$\eta(k(K-x))(-\gamma + q(x)) + kxg(x) \le k\xi(k(K-x))p(x).$$

In particular, when $\eta(y) = \xi(y) = y$, (5.2) is equivalent to

$$(K-x)(-\gamma + q(x)) + xg(x) \le k(K-x)p(x).$$

Hence, $k \ge \frac{1}{p(x)}[(-\gamma + q(x)) + \frac{xg(x)}{K-x}]$. Therefore, if we let $k = \max_{x \in [x^*, K]} \frac{1}{p(x)}[(-\gamma + q(x)) + \frac{xg(x)}{K-x}]$, then k satisfies (5.2).

LEMMA 5.2. *Denote* $\tilde{x} = \min\{x \mid x > x^*,\ \frac{xg(x)}{p(x)} = \frac{x^*g(x^*)}{p(x^*)}\}$ *and* $D = \{(x,y) \mid x^* \le x \le \tilde{x}, \xi(y^*) \le \xi(y) \le \frac{xg(x)}{p(x)}\}$. *Suppose*

(H9) $\frac{xg(x)}{p(x)} \le \frac{x^*g(x^*)}{p(x^*)}$ *when* $0 < x < x^*$.

Then all the limit cycles of (5.1) surrounding E^* *must envelope the region* D.

Proof. Let L be any limit cycle of (5.1) surrounding E^*. We note that L intersects the curve (the prey isocline) $\xi(y) = xg(x)/p(x)$, $0 < x < K$, exactly at two points, one in the region $0 < x < x^*$, the other in the region $x^* < x < K$. This is because when the two curves intersect, at the point of intersection $\left|\frac{dy}{dx}\right| = \infty$ on L, whereas the slope of $\xi(y) = xg(x)/p(x)$ at the same point is finite. Suppose they intersect at more than two points at any one of the two regions mentioned above, say in the region $x^* < x < K$ (the other region can be discussed similarly). In this region $\frac{dy}{dt} > 0$, and $\frac{dy}{dx} = 0$ if and only if $x = x^*$. Let p_1, p_2 be

the two intersection points in the order of counterclockwise. Then $\frac{dy}{dx}\big|_{p_1} = +\infty$ and $\frac{dy}{dx}\big|_{p_2} = -\infty$ for L. However, at the intersection point p_2, the slope of L should not be less than those of $\xi(y) = xg(x)/p(x)$ respectively. This contradicts the fact that $\frac{dy}{dx}\big|_{p_2} = -\infty$ for L.

Furthermore, it is easy to observe the following by Lemma 4.1. Let $A_0 = (x^*, y_0)$, and $\tilde{A}_0 = (x^*, \tilde{y}(y_0))$, such that both A_0 and $\tilde{A}_0$ lie on the same periodic curve of the following system

$$\begin{aligned} \dot{x} &= p(x)\Big(\frac{x^* g(x^*)}{p(x^*)} - \xi(y)\Big) \qquad & x^* = x(0) > 0 \\ \dot{y} &= \eta(y)(-\gamma + q(x)) & y_0 = y(0) > 0. \end{aligned} \tag{5.4}$$

Then it is easy to see that $\frac{d\tilde{y}(y_0)}{dy_0} \leq 0$, or more precisely, the bigger the y_0, the smaller the $\tilde{y}(y_0)$ where $y_0 > 0$, $y_0 \neq y^*$, and $\tilde{y}(\tilde{y}(y_0)) = y_0$.

Suppose the lemma is not true. Then $(\tilde{x}, y^*)$ is outside the region bounded by L. Let $A_0 = (x^*, y_0)$ be a point of L such that $y_0 < y^*$, and $\tilde{A}_0$ is defined as above. Further, let $A_1 = (x^*, y_1)$ be the other point of L such that $y_1 > y^*$. Then, we claim: $y_1 > \tilde{y}(y_0)$.

Let

$$\begin{aligned} \vec{v}_1(x,y) = \vec{v}_1 &= \Big(p(x)\Big(\frac{xg(x)}{p(x)} - \xi(y)\Big),\ \eta(y)(-\gamma + q(x)),\ 0\Big) \\ \vec{v}_2(x,y) = \vec{v}_2 &= \Big(p(x)\Big(\frac{x^* g(x^*)}{p(x^*)} - \xi(y)\Big),\ \eta(y)(-\gamma + q(x)),\ 0\Big). \end{aligned}$$

We have the following

$$\vec{v}_1 \times \vec{v}_2 = \Big(0,\ 0,\ \eta(y)(-\gamma + q(x))\Big(\frac{xg(x)}{p(x)} - \frac{x^* g(x^*)}{p(x^*)}\Big)\Big),$$

where $\vec{v}_1 \times \vec{v}_2$ is the vector cross product.

When $x^* \le x \le \tilde{x}$, we have

$$\eta(y)(-\gamma + q(x))\Big(\frac{xg(x)}{p(x)} - \frac{x^*g(x^*)}{p(x^*)}\Big) \ge 0. \tag{5.5}$$

Equality in (5.5) holds if and only if $x = x^*$, or $x = \tilde{x}$. Geometrically, (5.5) implies that the flow of (5.1) is always directed outwards with respect to the flow of (5.4). Hence $y_1 > \tilde{y}(y)_0$.

Replacing y_0 by y_1. We denote $A_{10} = (x^*, y_1) = A_1$ and $\tilde{A}_{10} = (x^*, \tilde{y}(y_1))$, $A_2 = (x^*, y_2) = A_0 = (x^*, y_0)$. Since (5.5) is also true when $0 < x < x^*$, by a similar argument as above, we conclude that $y_2 \le \tilde{y}(y_1)$. However, $\tilde{y}(y_1) < y_0$ since $y_1 > \tilde{y}(y_0)$. Hence $y_2 \le \tilde{y}(y_1) < y_0$. But $y_2 = y_0$, a contradiction.

Combining Lemma 5.1 and Lemma 5.2, we have the following:

THEOREM 5.3. *Let (H1) to (H8) hold for system (5.1), and $k > 0$ be a constant such that when $x \ge x^*$*

$$k\xi(k(K-x))p(x) \ge kxg(x) + \eta(k(K-x))(-\gamma + q(x)).$$

Let I, $\tilde{x}$, D be defined as in Lemma 5.1 and Lemma 5.2 respectively. Then the limit cycles of (5.1) will be contained in I and envelops D.

In particular, when $\xi(y) = \eta(y) = y$, we have:

COROLLARY 5.4. *Let* $k = \max_{x\in[x^*,K]} \frac{1}{p(x)}\left[(-\gamma+q(x)) + \frac{xg(x)}{K-x}\right]$ *and* I, $\tilde{x}$, D *be as in Lemma 5.1 and Lemma 5.2 respectively. Then the limit cycles of (5.1) will be contained in* I *and envelops* D.

Remark 5.1. Lemma 5.2 is more general than a similar result stated in Liou and Cheng (1987), where $p(x) = x$, and $g(x)$ is required to be strictly concave down.

Remark 5.2. A similar result as in Lemma 5.2 can be obtained. If we assume $\frac{xg(x)}{p(x)} \leq \frac{x^*g(x^*)}{p(x^*)}$ when $x^* < x < K$. Define

$$\tilde{x} = \max\left\{x \mid 0 < x < x^*,\ \frac{xg(x)}{p(x)} = \frac{x^*g(x^*)}{p(x^*)}\right\}$$

and

$$D = \{(x,y) \mid \tilde{x} \leq x \leq x^*, \xi(y^*) \leq \xi(y) \leq \frac{xg(x)}{p(x)}\}.$$

Then, all the limit cycles of (5.1) (if any) surrounding E^* must envelope the region D. however, in this case (H8) fails to hold, and E^* is stable instead of unstable.

Remark 5.3. The technique utilized in the proofs of Lemma 5.1 and 5.2 can be applied in other situations to obtain various other results. For example, let us consider the following Kolmogorov system (Freedman, 1980, Ch. 5)

$$\begin{aligned} \dot{x} &= xf(x,y), \qquad x_0 = x(0) > 0 \\ \dot{y} &= yg(x,y), \qquad y_0 = y(0) > 0. \end{aligned} \tag{5.6}$$

From the proof of Lemma 4.1, we note the solutions of

$$\begin{aligned} \dot{x} &= xf(x^*,y) \qquad x_0 = x(0) > 0 \\ \dot{y} &= yg(x,y^*) \qquad y_0 = y(0) > 0 \end{aligned} \tag{5.7}$$

are all periodic, where $E^*(x^*, y^*)$ is an equilibrium of (5.6). Let

$$\vec{v}_1 = (xf(x,y),\ yg(x,y), 0)$$

$$\vec{v}_2 = (xf(x^*,y),\ yg(x,y^*), 0).$$

Since $\vec{v}_1 \times \vec{v}_2 = (0, 0, xy(f(x,y)g(x,y^*) - f(x^*,y)g(x,y)))$. Hence

(i) If

$$f(x,y)g(x,y^*) - f(x^*,y)g(x,y) < 0$$

in $\Delta \subset R^{2+} = \{(x,y) \mid x > 0, y > 0\}$, then $\Delta \subset A$, where A denotes the region attracted by $E^*(x^*,y^*)$ in (5.6). If $\Delta = R^{2+}$, then $E^*(x^*,y^*)$ is globally stable.

(ii) If $f(x,y)g(x,y^*) - f(x^*,y)g(x,y) > 0$ in $\Delta, \Delta \subset R^{2+}$ then, Δ is contained in the region repelled by $E^*(x^*,y^*)$. In this case, the flow of (5.6) is always directed outward with respect to the flow of (5.7).

It is easy to see that if the functions $f(x^*,y)$ and $g(x,y^*)$ are replaced by continuous functions $\alpha(y)$ and $\beta(x)$, conclusions similar to (i) and (ii) are still true.

5.3. Period of limit cycles

We first state two lemmas concerning the location of limit cycles of system (5.1). By combining the result obtained in Section 5.2, we are able to give a better estimation of the location of the limit cycles. However, in this section, we are more concerned with the period of the limit cycles.

In the remainder of this section we define

$$h(x) = xg(x)/p(x)$$

and $x^*, \tilde{x}, I, D$ are the same as in Section 5.2. Furthermore, we assume (5.1) satisfies (H1) to (H9).

We denote

$$a_1 = \max\{\xi^{-1}(h(x)) | \, x \in (0, K)\}$$

$$a_2 = \min\{\xi^{-1}(h(x)) | \, x \in (0, x^*)\}$$

$$a_3 = \xi^{-1}(h(x^*))$$

$$x_m = \min\{x | \; h(x) = \xi(a_1)\}$$

and denote $L_i((x_0, y_0))\, i = 1, 2, 3$ as the orbit of the following system

$$\begin{aligned} \dot{x} &= p(x)(\xi(a_i) - \xi(y)) \\ \dot{y} &= \eta(y)(-\gamma + q(x)) \\ x_0 &= x(0) > 0, \; y_0 = y(0) > 0, \; i = 1, 2, 3 \end{aligned} \tag{5.8$_i$}$$

starting at the point (x_0, y_0).

LEMMA 5.5. *Every limit cycle of (5.1) contains the sets S_1 and S_2, where*

$$S_1 = \{(x, y) | \, x^* \le x \le x_m, y = a_1\}$$

$$S_2 = \{(x, y) | \, (x, y) \in L_3((x^*, a_1)), 0 < x \le x^*\}.$$

Proof We note $\dot{y} \ge 0$, when $x^* \le x \le K$, by Theorem 5.3, we see that S_1 is contained in every limit cycle of (5.1). Since (x^*, a_1) is the endpoint of the line

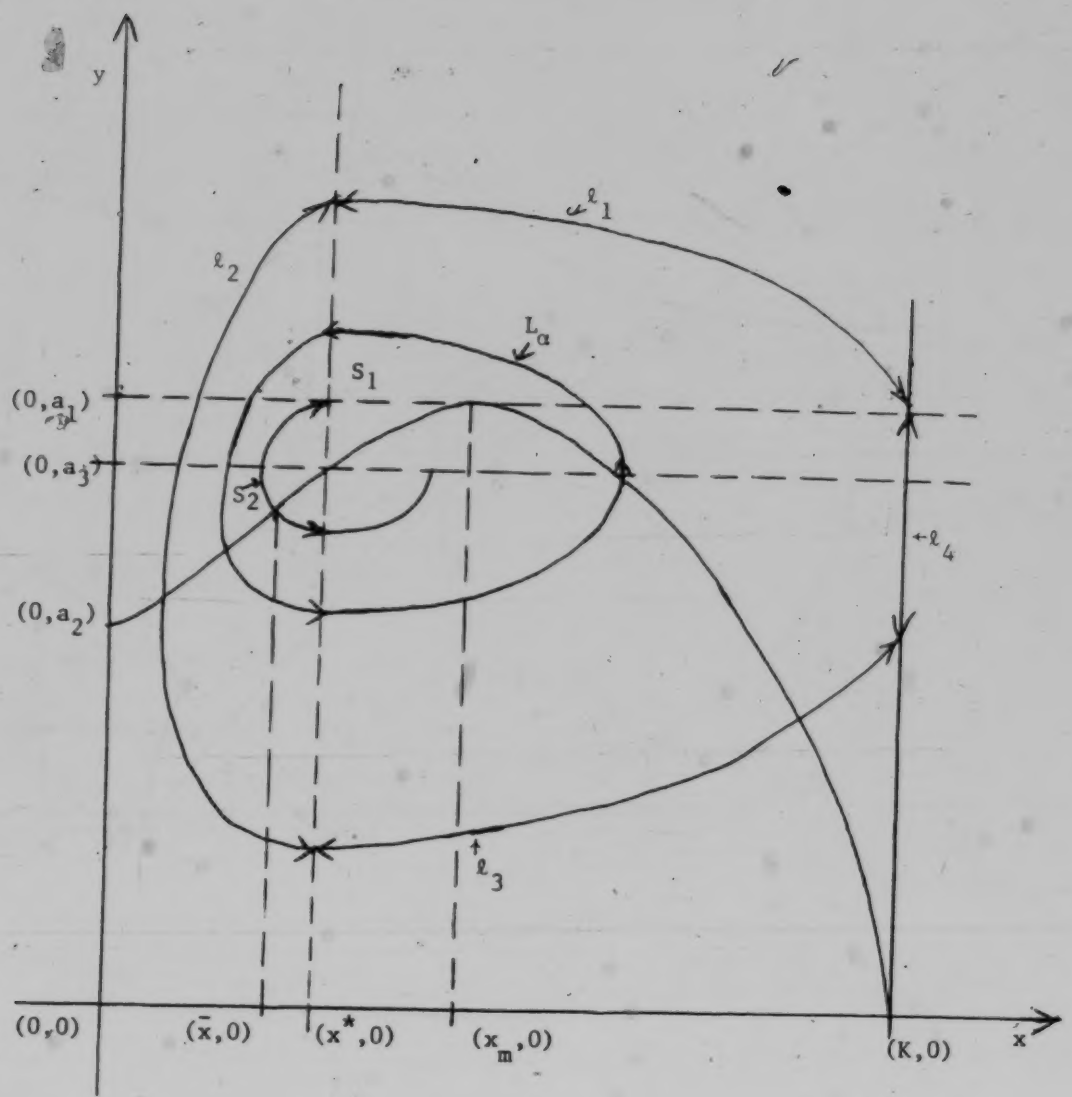

Figure 5.1 The illustration for locating limit cycles in system (5.1).

segment described by S_1, by the same technique as utilized in the proof of the Theorem 5.3, we know the flow of (5.1) is always directed outwards with respect to the flow of (5.8_3) in the region $0 < x \leq x^*$. This completes the proof. (See Fig. 5.1)

LEMMA 5.6. *All limit cycles of (5.1) are contained in the region bounded by the following four curves:*

$$\ell_1 = \{(x,y) | \, y \geq x^*, \, x^* \leq x \leq K, \, (x,y) \in L_1((K,a_1))\}$$

$$\ell_2 = \{(x,y) | \, 0 < x \leq x^*, \, (x,y) \in L_2((x^*,y_b)), y_b = \max\{y | \, (x,y) \in \ell_1\}\}$$

$$\ell_3 = \{(x,y) | \, x^* \leq x \leq K, \, (x,y) \in L_1((x^*,y_3)), \, y_3 = \min\{y | \, (x,y) \in \ell_2\}\}$$

$$\ell_4 = \{(x,y) | \, x = K\}$$

Proof Similar to the proof of Lemma 5.2. (See Fig. 5.1)

We are now in a position to consider the period of limit cycles of system (5.1). We denote $(\bar{x},\bar{y}) = S_2 \cap \{(x,y) | \, \xi(y) = h(x)\}$ where S_2 is defined as in Lemma 5.5. Further, we assume

(H10) $h'(x) \geq 0$, when $\bar{x} \leq x \leq x_m$.

Let $x_1 \in (x^*, x_m)$. Then when $x \geq x_1$,

$$\eta(y)(-\gamma + q(x)) \geq \eta(y)(-\gamma + q(x_1)) > 0. \tag{5.9}$$

(i) Assume (x_1, y_{1a}), $(x_1, y_{1b}) \in L_\alpha$, where $y_{1a} < y_{1b}$, and L_α is a limit cycle of (2.1). It is easy to see that the time spent by travelling from (x_1, y_{1a}) to (x_1, y_{1b}) is

$$T_1(L_\alpha) = \int_{y_{1a}}^{y_{1b}} \frac{dy}{\eta(y)(-\gamma + q(x))}.$$

By (5.9) we see

$$T_1(L_\alpha) < \int_{y_{1a}}^{y_{1b}} \frac{dy}{\eta(y)(-\gamma + q(x_1))} = G_1(L_\alpha, x_1). \tag{5.10}$$

We note further

$$\begin{aligned} 0 < G_1(L_\alpha, x_1) &= \Big(\int_{y_{1a}}^{y^*} + \int_{y^*}^{y_{1b}} \Big) \frac{dy}{\eta(y)(-\gamma + q(x_1))} \\ &< \frac{y^* - y_{1a}}{\eta(y_{1a})(-\gamma + q(x_1))} + \frac{y_{1b} - y^*}{\eta(y^*)(-\gamma + q(x_1))}. \end{aligned} \tag{5.11}$$

Let $x_2 \in (\overline{x}, x^*)$. Then when $x < x_2$,

$$\eta(y)(-\gamma + q(x)) < \eta(y)(-\gamma + q(x_2)) < 0. \tag{5.12}$$

(ii) Assume (x_2, y_{2a}), $(x_2, y_{2b}) \in L_\alpha$, where $y_{2a} < y_{2b}$ and L_α is the same as in (i).

Again, it is easy to see that the time spent by travelling from (x_2, y_{2b}) to (x_2, y_{2a}) is

$$T_2(L_\alpha) = \int_{y_{2b}}^{y_{2a}} \frac{dy}{\eta(y)(-\gamma + q(x))} = \int_{y_{2a}}^{y_{2b}} \frac{dy}{\eta(y)(\gamma - q(x))}.$$

By (5.12) we see that

$$T_2(L_\alpha) < \int_{y_{2a}}^{y_{2b}} \frac{dy}{\eta(y)(\gamma - q(x_2))} = G_2(L_\alpha, x_2). \tag{5.13}$$

Similar to (5.11) we have

$$\begin{aligned} 0 < G_2(L_\alpha, x_2) &= \Big(\int_{y_{2a}}^{y^*} + \int_{y^*}^{y_{2b}} \Big) \frac{dy}{\eta(y)(\gamma - q(x_2))} \\ &< \frac{y^* - y_{2a}}{\eta(y_{2a})(\gamma - q(x_2))} + \frac{y_{2b} - y^*}{\eta(y^*)(\gamma - q(x_2))}. \end{aligned} \tag{5.14}$$

(iii) The time spent by travelling from (x_1, y_{1b}) to (x_2, y_{2b}) is

$$T_3(L_\alpha) = \int_{x_1}^{x_2} \frac{dx}{p(x)(h(x) - \xi(y))} = \int_{x_2}^{x_1} \frac{dx}{p(x)(\xi(y) - h(x))}. \tag{5.15}$$

Further we note $p(x) > p(x_2)$ when $x > x_2$, and

$$\xi(y) - h(x) \geq \xi(y_{3b}(x)) - h(x) \geq 0, \qquad \overline{x} \leq x \leq x^*$$

where $(x, y_{3b}(x)) \in L_3((x^*, a_1))$, and $y_{3b}(x) > y^*$ and

$$\xi(y) - h(x) \geq \xi(a_1) - h(x) \geq 0, \qquad x^* \leq x \leq x_m.$$

Denote

$$0 < \delta_1(x_1, x_2) = \min\{\xi(y_{3b}(x)) - h(x),\ x_2 \leq x \leq x^*;\ \xi(a_1) - h(x_1)\}. \tag{5.16}$$

Then

$$p(x)(\xi(y) - h(x)) > p(x_2)\delta_1(x_1, x_2), \qquad x_2 < x < x_1,$$

hence

$$T_3(L_\alpha) < \int_{x_2}^{x_1} \frac{dx}{p(x_2)\delta_1(x_1, x_2)} = \frac{x_1 - x_2}{p(x_2)\delta_1(x_1, x_2)}. \tag{5.17}$$

We can refine the result (5.17) by splitting the integral (5.15) into two parts

$$T_3(L_\alpha) = \Big(\int_{x_2}^{x^*} + \int_{x^*}^{x_1} \Big) \frac{dx}{p(x)(\xi(y) - h(x))}. \tag{5.18}$$

Hence

$$\begin{aligned} T_3(L_\alpha) &\leq \int_{x_2}^{x^*} \frac{dx}{p(x)(\xi(y_{3b}(x)) - h(x))} + \int_{x^*}^{x_1} \frac{dx}{p(x)(\xi(a_1) - h(x))} \\ &< \int_{x_2}^{x^*} \frac{dx}{p(x_2)(\xi(y_{3b}(x)) - h(x))} + \int_{x^*}^{x_1} \frac{dx}{p(x^*)(\xi(a_1) - h(x))}. \end{aligned} \tag{5.19}$$

(iv) The time spent by travelling from $(x_2, y_{2\varepsilon})$ to $(x_1, y_{1\varepsilon})$ is

$$T_4(L_\alpha) = \int_{x_2}^{x_1} \frac{dx}{p(x)(h(x) - \xi(y))}. \tag{5.20}$$

Further, $p(x) > p(x_2)$ when $x > x_2$, and

$$h(x) - \xi(y) > h(x) - \xi(y_{3\varepsilon}(x)) \qquad x_2 < x \leq x^*$$

where $(x, y_{3\varepsilon}(x)) \in L_3((x^*, a_1))$, and $y_{3\varepsilon}(x) < y^*$, $y < y_{3\varepsilon}(x)$ when $x_2 < x \leq x^*$.

Similar to Lemma 5.5, we know that $L_3((\tilde{x}, y^*))$ is contained in all the limit cycles of (5.1). We denote $(x, \tilde{y}_{3\varepsilon}(x))$ as the points of $L_3((\tilde{x}, y^*))$, when $0 < x < \tilde{x}$, and $\tilde{y}_{3\varepsilon}(x) \leq y^*$.

Then

$$h(x) - \xi(y) > h(x) - \xi(\tilde{y}_{3\varepsilon}(x)), \qquad x^* < x < \tilde{x}.$$

Hence

$$T_4(L_\alpha) \leq \int_{x_2}^{x^*} \frac{dx}{p(x)(h(x) - \xi(y_{3\varepsilon}(x)))} + \int_{x^*}^{x_1} \frac{dx}{p(\tilde{x})(h(x) - \xi(\tilde{y}_{3\varepsilon}(x)))}. \tag{5.21}$$

Similarly, if we let

$$0 < \delta_2(x_1, x_2) = \min\{(h(x) - \xi(y_{3\varepsilon}(x)),\ x_2 \leq x \leq x^*,\ h(x) - \xi(\tilde{y}_{3\varepsilon}(x)),\ x^* \leq x \leq x_1\}$$

then

$$T_4(L_\alpha) \leq \frac{x_1 - x_2}{p(x_2)\delta_2(x_1, x_2)}. \tag{5.22}$$

We denote

$$G(L_\alpha, x_1, x_2) = G_1(L_\alpha, x_1) + G_2(L_\alpha, x_2) + \int_{x_2}^{x^*} \frac{dx}{p(x)(\xi(y_{3b}(x)) - h(x))}$$
$$+ \int_{x^*}^{x_1} \frac{dx}{p(x)(\xi(a_1) - h(x))} + \int_{x_2}^{x^*} \frac{dx}{p(x)(h(x) - \xi(y_{3s}(x)))} \tag{5.23}$$
$$+ \int_{x^*}^{x_1} \frac{dx}{p(x)(h(x) - \xi(\tilde{y}_{3s}(x)))}$$

and

$$G(L_\alpha) = \min\{G(L_\alpha, x_1, x_2) | x^* < x_1 < x_m,\ \bar{x} < x_2 < x^*\}$$
$$T(L_\alpha) = \sum_{i=1}^{4} T_i(L_\alpha),$$

i.e. the period of L_α. Then from (i), (ii), (iii) and (iv), we have the following theorem:

THEOREM 5.7. *$T(L_\alpha) < G(L_\alpha)$. Moreover, we have $y_{1b} < y_b, y_{1s} > y_s$ where y_b, y_s are defined as in Lemma 5.6. Therefore, if we denote*

$$E(x_1, x_2) = \frac{y^* - y_s}{\eta(y_s)(-\gamma + q(x_1))} + \frac{y_b - y^*}{\eta(y^*)(-\gamma + q(x_1))}$$
$$+ \frac{y^* - y_s}{\eta(y_s)(\gamma - q(x_2))} + \frac{y_b - y^*}{\eta(y^*)(\gamma - q(x_2))} \tag{5.24}$$
$$+ \frac{x_1 - x_2}{p(x_2)} \sum_{i=1}^{2} \frac{1}{\delta_i(x_1, x_2)}$$

and $E = \min\{E(x_1, x_2) | x^* < x_1 < x_m,\ \bar{x} < x_2 < x^*\}$. Then, $T(L_\alpha) < G(L_\alpha) < E$.

Remark 5.4. In the case that $L_3((\tilde{x}, y_1^*))$ contains D, we can get better estimation of the period if we replace $L_3((x^*, a_1))$ by $L_3((\tilde{x}, y^*))$. The $G(L_\alpha, x_1, x_2)$ function is explicitly computable. Of course, $E(x_1, x_2)$ is much easier to compute.

Remark 5.5. If we replace the line S_1 by the corresponding part of $L_3((x_m, a_1))$, i.e. $\overline{S}_1 = \{(x,y) | (x,y) \in L_3((x_m, a_1),\ x^* \leq x \leq x_m,\ y > y^*\}$, and replace S_2 by the corresponding left half part of $L_3((x_m, a_1))$, then Lemma 5.5 is still valid. In fact, this result is better than Lemma 5.5. This will also allow us to give a better estimation of the period of the limit cycles.

5.4. Discussion

In Theorem 3.6 of this thesis, we showed that in order to ensure the uniqueness of limit cycles in system (5.1), in addition to (H1)-(H8), we require the following inequality hold in $0 \leq x < x^*$ and $x^* < x \leq K$;

$$\frac{d}{dx}\left(\frac{p(x)\left(\frac{xq(x)}{p(x)}\right)'}{-\gamma + q(x)}\right) \leq 0. \tag{5.25}$$

By utilizing the results of section 5.2, we can improve the theorem by requiring (5.25) to hold only in $0 \leq x < x^*$ and $x_m \leq x \leq K$, where x_m is the same as defined in section 5.3. This is because the point (x_m, a_1) is contained in all the limit cycles of (5.1), and by virtue of the proof of Cherkas et al's theorem (see the appendix of chapter III), whether or not inequality (5.25) holds in $x^* < x < x_m$ does not affect the outcome of the theorem.

Since we know $(\tilde{x}, a_1)$ ($\tilde{x}$ is as defined in Lemma 5.2) is also contained in all the limit cycles of (5.1), by imposing some conditions on the prey isocline and $\xi(y)$ and $\eta(y)$, we can improve Theorem 3.6 in various ways, or obtain some variations of the above mentioned theorem. A good example of this is Liou and

Cheng's result in the case that $\xi(y) = \eta(y) = y$, $p(x) = x$, and the prey isocline is concave down.

As far as the periods of the limit cycles are concerned, the positive lower bounds can be derived in a similar way as we did for the upper bounds. It would be of interest if one can obtain some qualitative results for the periods of the limit cycles in Gause-type predator-prey systems as Hsu (1983) did for the Lotka-Volterra system.

CHAPTER VI

CONCLUDING DISCUSSION AND REMARKS

In this thesis, we have carried out a detailed global analysis of the Gause-type predator-prey system. In the preliminary chapter, we have listed a series of global stability results for the unique positive stable equilibrium. Throughout this thesis, our emphasis is those properties related to the limit cycles of this system.

We have always assumed the unique positive equilibrium is unstable in Chapter III, IV and V. However, this assumption is not necessary for a limit cycle to exist as pointed out by Wolkowicz (1987) utilizing the Hopf bifurcation theorem. It can be expected that without the instability assumption, any meaningful investigation concerning the properties of limit cycles will be very difficult. So for, these is very little has been done along this direction.

As pointed out by Ye et al (1986), over the last thirty years there has been tremendous progress in the theory of limit cycles, especially in quadratic differential systems. Nevertheless, there is hardly any progress achieved concerning the theory of limit cycles in Kolmogorov-type predator-prey systems. One of the difficulties is that the theorems developed for quadratic systems are not applicable in the Kolmogorov situation. Although we can derive some restrictive conditions for that system so as to make the technique of Cherkas et al applicable, it is to be expected that those conditions would be very complicated and very hard to satisfy. The author believes that new methods and ideas will be

required to develop an interesting, applicable and systematical theory of limit cycles in Kolmogorov predator-prey systems.

By a careful examination of Liou and Cheng's (1988) result and its proof, one can see that their result can be improved in the following ways:

(1) . The assumption (1) of Liou and Cheng's result can be replaced by: $g(x) \in C^1([0,\infty))$, $g(0) = 0$, $g(x) - \lambda > 0$, when $x > x^*$, and $g(x) - \lambda < 0$, when $0 < x < x^*$.

(2) . The assumption (2) can be replaced by: $f(x) \in C^2([0,\infty))$, $f(0) \geq 0$, $f'(0) > 0$ and there exists $K > 0$, such that $(x-K)f(x) < 0$ for $x \neq K$. There exists an α, $x^* < \alpha < \bar{x}^*$ (where $\bar{x}^* = f_2^{-1} \circ f_1(x^*)$ and $f_1 = f|_{(0,\alpha)}$, $f_2 = f|_{(\alpha,K)}$), such that $f'(x) > 0$ for $x^* < x < \alpha$, $f'(\alpha) = 0$ and $f'(x) < 0$ for $\alpha < x < \bar{x}^*$. This can be explained as follows: by the assumption (4) of section 3.2, we have

$$0 > \frac{d}{dx}\left(\frac{xf'(x)}{g(x)-\lambda}\right) = \frac{(f'(x)+xf''(x))(g(x)-\lambda) - g'(x)xf'(x)}{(g(x)-\lambda)^2}. \tag{6.1}$$

If there exists $\tilde{x}$, $0 < \tilde{x} < \alpha$ and $f'(\tilde{x}) = 0$, then there is a point $\tilde{x}_{min}$, such that

$$\tilde{x}_{min} = min\{x \mid 0 < x < \alpha,\ f'(x) = 0\}.$$

Hence $f'(\tilde{x}_{min}) = 0$ and $f''(\tilde{x}_{min}) \leq 0$, which implies

$$\frac{d}{dx}\left(\frac{xf'(x)}{g(x)-\lambda}\right)\Big|_{x=\tilde{x}_{min}} = \frac{xf''(x)}{g(x)-\lambda}\Big|_{x=\tilde{x}_{min}} \geq 0.$$

This contradicts (6.1). Similarly, we can exclude the possibility of there existing $\bar{x}$, such that $\alpha < \bar{x} < K$, and $f'(\bar{x}) = 0$.

In chapter IV, we have shown that the strict convexity (concave down) of the prey isocline does not guarantee the uniqueness of limit cycles in a Gause-type predator-prey system, thus disproving the conjecture posed by H.I. Freedman. However, the following two conjectures remain open.

Conjecture 1. (weak) Denote $h(x) = \frac{xg(x)}{p(x)}$ as the prey isocline of the Gause-type predator-prey system. Assume there is a constant α, $0 < \alpha < K$, such that $h'(x) > 0$ when $0 \leq x < \alpha$, $h'(x) < 0$ when $\alpha < x < K$. $h(x) \in C^1([0,\infty))$ and is symmetric with respect to the line $x = \alpha$. Then the corresponding predator-prey system has a unique limit cycle in the positive cone when its unique positive equilibrium is unstable.

Conjecture 2. (strong) In addition to all the assumptions made in conjecture 1, we assume further that $h(x) \in C^2([0,\infty))$ and $h''(x) \leq 0$. Then the corresponding Gause-type predator-prey system has a unique limit cycle in the positive cone when its unique positive equilibrium is unstable.

These two conjectures are motivated partially by the work of Conway and Smoller (1986), where they considered the following so-called "asocial" predator-prey system,

$$\begin{aligned} \dot{u} &= u(f(u) - v) \\ \dot{v} &= v(u - \gamma) \end{aligned} \tag{6.2}$$

subject to the following assumptions:

(A) $f(b) = f(K) = 0$, where $0 < b < K$; $f(\mu)$ is positive for $b < u < K$ and negative otherwise,

(B) $f'(u) > 0$ on $[b, m)$, $f'(u) < 0$ on $(m, K]$, $f'' < 0$ and $f'''(m)$ exists,

(C) $b < \gamma < K$.

An important proposition they claimed is: *If $f(u)$ is symmetric about $u = m$, then every periodic orbit of (6.2) is an orbitally stable attractor, and thus there can be at most one such orbit.*

Unfortunately, their proof (using the same method as Cheng (1981)) is not correct. To ensure that the proof is valid the following assumption will be sufficient:

(D) $\frac{d}{du}\left(\frac{uf'(u)}{u-\gamma}\right) \leq 0$.

However, as we pointed out earlier, conditions like (D) may not necessary, and therefore the claim made by Conway and Smoller may still be true. This serves as the background for proposing conjecture 2. From the procedure of constructing the counterexample presented in chapter IV, the author gained the feeling that even without the convexity, conjecture 2 may still be true, which suggests to the author to pose it as conjecture 1.

For the following Lotka-Volterra predator-prey system

$$\begin{aligned} \dot{x} &= x(\alpha - \beta y), \quad x(0) = x_0 > 0 \\ \dot{y} &= y(\delta x - y), \quad y(0) = y_0 > 0 \end{aligned} \tag{6.3}$$

Hsu (1983) has obtained the following result concerning the period of the orbit of (6.3).

Let C_0 be the energy level for the periodic orbit, and $T(C_0)$ be the period of the orbit, then $T(C_0)$ is a strictly increasing function on $(0, \infty)$ with $\lim_{C_0 \to \infty} T(C_0) = +\infty$, *and* $\lim_{C_0 \to 0} T(C_0) = 2\pi/\sqrt{\alpha\gamma}$.

In the Gause-type predator-prey system, we consider the following poincare map (assuming (x^*, y^*) is unstable):

$$P : (x^*, y(0)) \to (x^*, y(T(y(0)))$$

where $0 < y(0) < y^*$ and $0 < y(T(y(0))) < y^*$. Here $(x^*, y(T(y(0)))$ is the first returning point of the orbit of Gause-type predator-prey system starting at the point $(x^*, y(0))$ and $T(y(0))$ is the time spent. It will be very interesting if one can prove the following conjecture:

Conjecture 3. $T(y(0))$ is a strictly decreasing function on $(0, y^*)$ in the case that the unique positive equilibrium (x^*, y^*) is unstable.

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APPENDICES

In these appendices, various results of analysis and differential equations are given, which are crucial to the understanding of the material in this text.

Appendix A

Existence, uniqueness and continuity of solutions of ordinary differential equations

A.1 Existence

The question of existence relevant to this text has to do with the so-called initial value problems of ordinary differential equatins. We consider the system

$$\dot{x} = f(t, x) \tag{A.1}$$

where x is an n-dimensional vector, t a scalar, and f an n-dimensional vector each component of which is a function of $(n+1)$ variables. We wish to consider solutions of (A.1) which satisfy the initial condition

$$x(t_0) = x_0 \tag{A.2}$$

where x_0 is a specified n-dimensional vector, and the question of whether or not solutions of (A.1) subject to (A.2) exist is the question of interest.

The following, known as the Cauchy-Peano existence theorem, is the most relevant existence theorem for our purposes.

THEOREM A.1. *(Cuachy-Peano) Let R be the rectangle, $R: |t - t_0| \leq a$, $||x - x_0|| \leq b$ $(a, b > 0)$. Let f be continuous over R and let $M = max\{||f(t,x)|| \mid (t,x) \in R\}$ and let $\alpha = min(a, b/M)$. Then there exists a differentiable function $x(t)$ which is a solution of (A.1) on the interval $|t - t_0| \leq \alpha$ and which satisfies (A.2).*

See Hartman (1964) for a proof of this theorem.

In connection with the question of existence there occurs the question of extendibility. The reader is referred to Hartman (1964) for extendibility theorems and for more general existence theorems.

A.2 Uniqueness

For purpose of modeling in mathematical ecology we want our models to have unique solutions. To this end, we usually require the $f(t,x)$ in (A.1) to possess the Lipschitz property with respect to x.

Let $f(t,x)$ be a function defined in some set $I \times J$. Then $f(t,x)$ is uniformly Lipschitz continuous with respect to x, if

$$||f(t,x_1) - f(t,x_2)|| \leq k||x_1 - x_2||, \text{ for all } (t,x_1),(t,x_2) \in I \times J.$$

Note that a differentiable function on $I \times J$ is automatically Lipschitzian and a Lipschitz function is automatically continuous. The following is the most important uniqueness theorem for our purposes.

THEOREM A.2. *Let R, M and α be as in A.1. Assume for each fixed x, $f(t,x)$ is continuous in t and for each fixed t, $f(t,x)$ is Lipschitzian in x, $(t,x) \in R$. Then there is a unique, continuously differentiable solution of (A.1) on the interval $|t - t_0| < \alpha$ and which satisfies (A.2).*

Again for a proof see Hartman (1964). Also, the property of $f(t,x)$ being Lipschitzian in x will be automatically fulfilled if each component of $f(t,x)$ possesses bounded partial derivatives with respect to the components of x in R.

A.3 Continuity

Let $f(t,x)$ be continuous on a (t,x)-set E and let $x = x(t)$ be a solution of (A.1) on an interval J. The interval J is called a right maximal interval of existence for x if there does not exist an extension of $x(t)$ over an interval J_1 so that $x = x(t)$ remains a solution of (A.1); J is a proper subset of J_1; J, J_1 have different right endpoints. A left maximal interval of existence for x is defined similarly. A maximal interval of existence is an interval which is both a left and right maximal interval.

Form now on, we assume the initial value problem (A.1) and (A.2) has a unique solution $x(t) = \eta(t, t_0, x_0)$ which is defined on a maximal t-interval

(w_-, w_+) where $w_\pm$ depends on (t_0, x_0). In this section, we consider the continuity of $\eta(t, t_0, x_0)$ in E.

Often, a more general situation is encountered in which (A.1) is replaced by a family of initial value problems depending on a set of parameters $z = (z_1, \ldots, z_e)$,

$$x' = f(t, x, z) \text{ and } x(t_0) = x_0 \tag{A.3}$$

where for each fixed z, (A.3) has a unique solution $x(t) = x(t, t_0, y_0, z)$.

The following continuity theorem is sufficient for our purpose.

THEOREM A.3. *Let $f(t, x, z)$ be continuous on an open (t, x, z)-set E with the property that for every $(t_0, x_0, z) \in E$, the initial value problem (A.3), with z fixed, has a unique solution $x(t) = \eta(t, t_0, x_0, z)$. Let $w_- < t < w_+$ be the maximal interval of existence of $x(t) = \eta(t, t_0, x_0, z)$. Then $w_+ = w_+(t_0, x_0, z)$ [or $w_- = w_-(t_0, x_0, z)$] is a lower [upper] semicontinuous function of $(t_0, x_0, z) \in E$ and $\eta(t, t_0, x_0, z)$ is continuous on the set $w_- < t < w_+$, $(t_0, x_0, z) \in E$.*

Again for a rigorous proof of this theorem see Hartman (1964), where results on differentiability also available.

Appendix B

Autonomous systems - limit sets, invariant sets, stability of solutions, Lyapunov functions

B.1 Limit sets, invariant sets

A system of differential equations in which the independent variable t does not occur explicitly,

$$\dot{x} = f(x) \tag{B.1}$$

is called autonomous. A trivial but important property of such systems is the fact that if $x = x(t)$, $\alpha < t < \beta$, is a solution of (B.1), then $x = x(t+t_0)$ is also a solution for $\alpha - t_0 < t < \beta - t_0$ for any constant t_0. An orbit will mean a set of points x on a solution $x = x(t)$ of (B.1) without reference to a parameterization.

Any system $\dot{x} = f(t,x)$ can be considered autonomous if the dependent variable x is replaced by the $(d+1)$-vector (t,x) and the sytem $x' = f(t,x)$ is replaced by $t' = 1$, $x' = f(t,x)$.

A point x^* is called an equilibrium (or stationary, or singular point, or stead state etc.) of (B.1) if $f(x^*) = 0$, and a regular point if $f(x^*) \neq 0$. The equilibrium x^* is characterized by the fact that the constant $x(t) = x^*$ is a solution of (B.1).

For definitions of w-limit and α-limit points and limit points, see section 2.7, Definition 2.3

A set M in R^n is called an invariant set of (B.1) if, for any p in M, the solution $\eta(t,p)$ of (B.1) such that $\eta(0,p) = p$ belongs to M for $t \in (-\infty,\infty)$, i.e. $\eta(t,p) \in M$, for $t \in (-\infty,\infty)$. Any orbit of (B.1) is obviously an invriant set of (B.1). A set M is called positively (negatively) invariant if for each p in M, $\eta(t,p)$ belongs to M for $t \geq 0$ $(t \leq 0)$. The following theorem describes some properties of limit point sets.

THEOREM B.1. *The α- and w-limit sets of an orbit γ are closed and invariant. Furthermore, if $\gamma^+(\gamma^-)$ is bounded, then the $w-(\alpha-)$ limit set is nonempty compact, connected, dist$(\eta(t,p), w(\gamma(p))) \to 0$ as $t \to \infty$ and dist$(\eta(t,p), \alpha(\gamma(p))) \to 0$ as $t \to -\infty$.*

B.2 Linear equations, variational equations, stability and Lyapunov functions

The general linear system with constant coefficients may be written in the form

$$x' = Ax \tag{B.2}$$

where x is the n-dimensional vector whose i-th component is x_i and A is the $n \times n$ matrix whose ij-th component is a_{ij}.

The solution of (B.2) subject to $x(0) = x_0$ is

$$x = e^{A(t-t_0)}\, x_0 \tag{B.3}$$

where by e^M, M an $n \times n$ matrix, we mean the convergent series

$$e^M = \sum_{k=0}^{\infty} \frac{M^k}{k!}. \tag{B.4}$$

We are interested in the stability of the zero solution ($x_0 = 0$). $x = 0$ is said to be <u>stable</u> if given any $\epsilon > 0$, there is a $\delta > 0$ such that all solutions $x(t)$ for which $||x(t_0)|| < \delta$ for some t_0, then $||x(t)|| < \epsilon$ for $t \geq t_0$. In addition, if $\lim_{t\to\infty} x(t) = 0$, then $x = 0$ is said to be <u>asymptotically stable</u>. If $x = 0$ is not stable, it is said to be <u>unstable</u>.

The following criteria tell the complete story for system (B.2).

THEOREM B.2. *If all eigenvalue of A have negative real parts, $x = 0$ is asymptotically stable. If one eigenavlue of A has positive real part, $x = 0$ is unstable. If no eigenvalues have positive real parts, but one or more have zero real parts, then if the eigenvalues with zero real parts have simple elementary divisors (i.e., there are as many independent eigenvectors belonging to each of those eigenvalues*

as their respective multiplicities), $x = 0$ is stable, but if any of the eigenvalues with zero real parts do not have simple elementary divisors, $x = 0$ is unstable.

Now we consider the following autonomous system

$$\dot{x} = f(x) \tag{B.5}$$

and let $\phi(t)$ be a solution of this system, i.e., $\dot{\phi}(t) = f(\phi(t))$. The variational equation of (B.5) with respect to $\phi(t)$ is the linear part of the expansion of system (B.5) about $\phi(t)$. It is of the form

$$\dot{y} = f_x(\phi(t))y \tag{B.6}$$

where the variational matrix $f_x(\phi(t))$ is the matrix whose ij-th component is $(\partial f_i/\partial x_j)(\phi(t))$.

Under certain circumstances the stability of $y = 0$ of (B.6) determines the stability of $x = \phi(t)$ of (B.5). In the special case that $\phi(t) = \phi_0$, a constant, then if we set $A = f_x(\phi_0)$, system (B.6) reduces to (B.2) with x replaced by y. Since (B.6) can be regarded as a small perturbation of (B.5), it can be shown that if the eigenvalues of A all have negative real parts, then both $y = 0$ and $x = \phi_0$ are asymptotically stable solutions of (B.6) and (B.5), respectively. If one of the eigenvalues of A has a positive real part, then both of the preceeding solutions are unstable. In the case that one or more of the eigenvalues of A have zero real parts (and the rest have negative real parts), the analysis is considerably more complicated. The reader is referred to Hartman (1964), or Nemytskii and Stepanov (1960).

In case $\phi(t)$ is periodic, the reader is referred to the Floquet theory in Hartman(1964). A brief discussion of stabiity of periodic solutions is included in section 7 of chapter II.

Let $V(x)$ be a scalar function of the n components of x. By $\dot{V}(x)$,the derivative of V along solutions of system (B.5), we mean

$$\dot{V}(x) = \sum_{i=1}^{n} \frac{\partial V(x)}{\partial x_i} f_i(x)\,. \tag{B.7}$$

$V(x)$ is said to be positive definite function if $V(0) = 0$, and outside the origin, but inside some domain D containing the origin, $V(x) > 0$.

Suppose $f(0) = 0$ in (B.5). The following results give stability criteria for $x = 0$ of system (B.5).

THEOREM B.3. *Let $V(x)$ be a positive definite function in an open set D. Let $\Omega \subset D$ be a subregion of D containing the origin in its interior.*

(i) If $\dot{V}(x) \leq 0$, $x \in \Omega$, then $x = 0$ is stable.

(ii) If $\dot{V}(x) < 0$, $x \in \Omega$, then $x = 0$ is asymptotically stable.

(iii) If $\dot{V}(x) > 0$, then $x = 0$ is unstable.

In the case $\dot{V}(x) \leq 0$, $V(x)$ is called a Lyapunov function.

Appendix C.

The Poincaré-Bendixon theorem

The Poincaré-Bendixon theorem is one of the best-known theorems for showing the existence of limit cycles of an autonomous system of differential equations of two dimensions. As usual, existence and uniqueness of solutions to initial value problem are assumed. We also assume solutions are extendible, i.e. they exist for all time.

The theorem arises as a consequence of the uniqueness of solutions, which implies that in the phase plane,solutions may not intersect with themselves unless they are periodic or connect with equilibria.

THEOREM C.1. *(Poincaré-Bendixon) Let* Γ *be a solution of (B.5) (in two dimensions) and from some time on, the orbit of* Γ *lies in a closed and bounded set in the plane. If the w-limit points set of* Γ *does not contain any eqilibria, then either* Γ *is the periodic orbit or* Γ *appraoches a periodic orbit asymptotically.*

An analysis and proof of the Poincaré-Bendixon theorem can be found in Chapter VII of Hartman (1964).

Appendix D

The Hopf-Bifurcation Theorem

In this section, we present an alternative way of showing the existence of limit cycles (or periodic solutions) in an autonomous system, namely, the Hopf-Bifurcation theorem. It is valid for any finite dimensional autonomous sytem.

We consider the following system

$$\frac{dx}{dt} = F(x,\mu),\ x \in R^n. \tag{D.1}$$

The proof of the following nonanalytic version of Hopf bifurcation theorem can be found in the book of Hassard et al (1981).

THEOREM D.1. *Suppose in (D.1)*

(1) $F(0,\mu) = 0$ *for* μ *in an open interval containing zero, and* $0 \in R^n$ *is an isolated equilibrium of (D.1).*

(2) $F(x,\mu) \in C^{L+2}(R^n \times R^1)$, $L \geq 2$.

(3) $A(\mu) = D_x F(0,\mu) = \left(\overline{\frac{\partial F_i}{\partial x_j}}(0,u)\right)_{n\times n}$ *has a pair of complex conjugate eigenvalues* λ *and* $\bar{\lambda}$ *such that*

$$\lambda(\mu) = \alpha(\mu) + i\omega(\mu)$$

where $\omega(0) = \omega_0 > 0$, $\alpha(0) = 0$, $\alpha'(0) \neq 0$.

(4) The remaining $n-2$ *eigenvalues of* $A(0)$ *have strictly negative real parts, then (D,1) has a family of periodic solutions such that there eixsts an* $\epsilon_p > 0$ *and a* C^{L+1} *-function* $\mu^p(\epsilon)$,

$$\mu^p(\epsilon) = \sum_{1}^{[\frac{L}{2}]} \mu_{2i}^p \epsilon^{2i} + o(\epsilon^{L+1}) \quad (0 < \epsilon < \epsilon_p) \tag{D.2}$$

such that for each $\epsilon \in (0,\epsilon_p)$ *there exists a periodic solution* $p_\epsilon(t)$, *occuring for* $\mu = \mu^\gamma(\epsilon)$. *There is a neighborhood* η *of* $x = 0$ *and an open interval* J *containing* o, *such that for any* $\mu \in J$ *the only nonconstant periodic solutions of (D.1) that*

lie in η are members of the family $p_\epsilon(t)$ for values of ϵ satisfying $\mu^p(\epsilon) = \mu$, $\epsilon \in (0, \epsilon_p)$. The period $T^p(\epsilon)$ of $p_\epsilon(t)$ is a C^{L+1}-function

$$T^p(\epsilon) = \frac{2\pi}{w_0}\left[1 + \sum_1^{[\frac{L}{2}]} \tau_{2j}^p \epsilon^{2i}\right] + o(\epsilon^{L+1}),\ (0 < \epsilon < \epsilon_p) \tag{D.3}$$

Exactly two of the Floquet exponents of $p_\epsilon(t)$ approach zero as $\epsilon \downarrow 0$. One is 0 for $\epsilon \in (0, \epsilon_p)$, and the other is a C^{L+1} function

$$\beta^p(\epsilon) = \sum_1^{[\frac{L}{2}]} \beta_{2i}^p \epsilon^{2i} + o(\epsilon^{L+1})\ (0 < \epsilon < \epsilon_p). \tag{D.4}$$

The periodic solution $p_\epsilon(t)$ is orbitally asymptotically stable with asymptotic phase if $\beta^p(\epsilon) < 0$ but is unstable if $\beta^p(\epsilon) > 0$. If there exists a first nonvanishing coefficient μ_{2k}^p $(1 \le K \le [L/2])$, then there is an $\epsilon_1 \in (0, \epsilon_0]$ such that the open interval

$$J_1 = \{\mu | 0 < \mu/\mu_{2k}^p < \mu^p(\epsilon_1)/\mu_{2k}^p\} \tag{D.5}$$

has the following properties. For any μ in J_1 there is a unique $\epsilon \in (0, \epsilon_1)$ for which $\mu^p(\epsilon) = \mu$. Hence the family of periodic solutin $p_\epsilon(t)$ $(0 < \epsilon < \epsilon_1)$ may be parameterized as $p(t, \mu)$ $(\mu \in J_1)$. For $\mu \in J_1$, the period $T(\mu)$ and Floquet exponent $\beta(\mu)$ are C^L-function of $|\mu|^{1/k}$. The first nonvanishing coefficient β_{2k}^p is given by

$$\beta_{2k}^p = -2\alpha'(0)\mu_{2k}^p \tag{D.6}$$

and sign $\beta(\mu) =$ sign β_{2k}^p, thus the members $p(t, \mu)$ $(\mu \in J_1)$ of the family of periodic solutions are asymptotically stable if $\beta_{2k}^p < 0$ and are unstable if $\beta_{2k}^p > 0$.

Appendix E

The Poincaré map

We consider the following autonomous differential equation system

$$x' = f(x),\ x \in R^n \tag{E.1}$$

Denote $\eta(x_0,t)$ as the solution of (E.1) such that $\eta(x_0,0) = x_0$, and let $\gamma(t)$ be a closed orbit of (E.1) such that $\gamma(t+\tau) = \gamma(t)$ for all $t \in R$ and τ is the least period. Assuming $f \in C^1$, then the image of γ is clearly diffeomorphic to the circle.

Definition Let γ be a closed orbit described as above, let $m \in \gamma$, say $m = \gamma(0)$ and let S be a local transversal section; i.e. a submanifold of codimension one transverse to γ (i.e. $\gamma'(0)$ is not tangent to S). Let $\mathcal{D} \subset R^n \times R$ be the domain on which the flow is defined.

A Poincaré map of γ is a mapping $P : W_0 \to W_1$ where:

(P1) $W_0, W_1 \subset S$ are open neighborhoods of $m \in S$, and P is a C^k diffeomorphism;

(P2) there is a function $\delta : W_0 \to R$ such that for all $x_0 \in W_0$, $(x_0, \tau - \delta(x_0)) \in \mathcal{D}$ and $P(x_0) = \eta(x_0, \tau - \delta(x_0))$; and finally,

(P3) if $t \in (0, \tau - \delta(x_0))$, then $\eta(x_0,t) \notin W_0$.

The reader is referred to Marsden and McCracken's book (1976) for a detailed account of the theorem and proof of the existence and uniqueness of Poincaré maps.

Appendix F

Persistence

For the basic definitions and results concerning a flow $F = (E, R, \pi)$ where E is a closed subset of a locally compact metric space (ξ, d), we refer to Bhatia and Szegō (1967). We shall use S^0, ∂S to denote its interior and boundary, respectively. We assume F is continuous and ∂E is invariant under F. That is $\pi : E \times R \to E$ is continuous map such that $\pi(\pi(x,t),s) = \pi(x,t+s)$ for all $x \in E$, $s,t \in R$, and $\pi(\partial E \times R) \subset \partial E$. For example, we might have $\xi = R^n$, $E = R^n_+$, the nonnegative cone in R^n and $x \in E$ represents n component populations whose interactions are modeled by the flow F.

Definition F.1 F will be called weakly persistent if for all $x \in E^0$, $\overline{\lim}_{t\to\infty} d(\pi(x,t), \partial E) > 0$.

Definition F.2 F will be called persistent if for all $x \in E^0$, $\underline{\lim}_{t\to\infty} d(\pi(x,t), \partial E) > 0$.

Definition F.3 F will be called uniformly persistent if there exists $\epsilon_0 > 0$ such that for all $x \in E^0$, $\underline{\lim}_{t\to\infty} d(\pi(x,t), \partial E) \geq \epsilon_0$.

For an excellent account of the persistence theory, the reader is referred to Butler, Freedman and Waltman (1986) or Butler and Waltman (1986).